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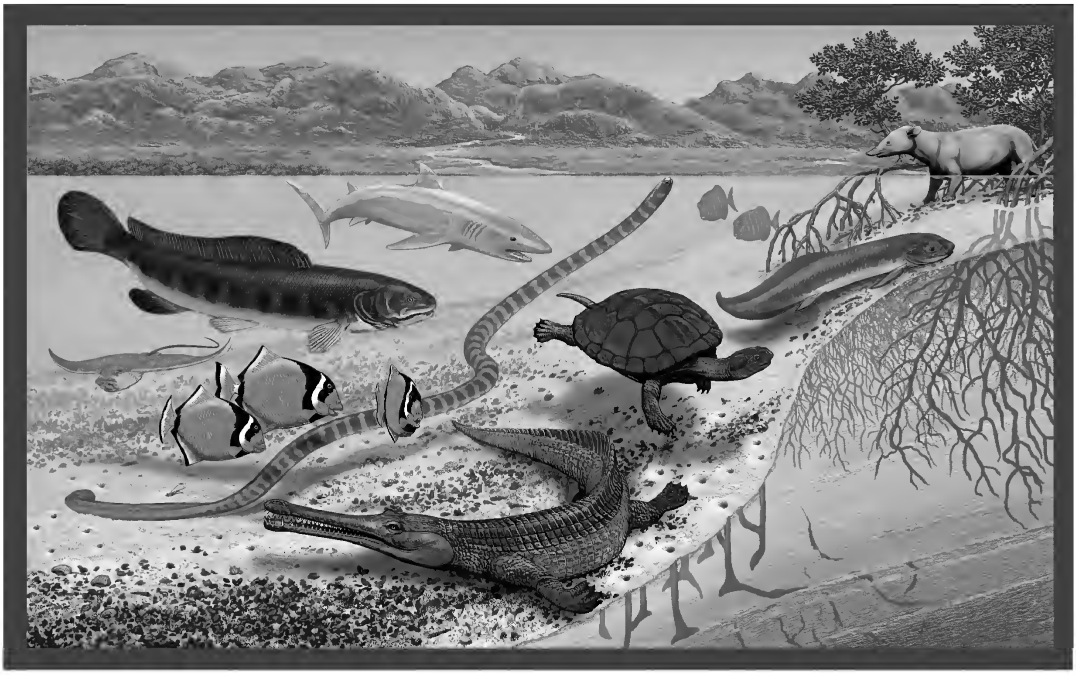

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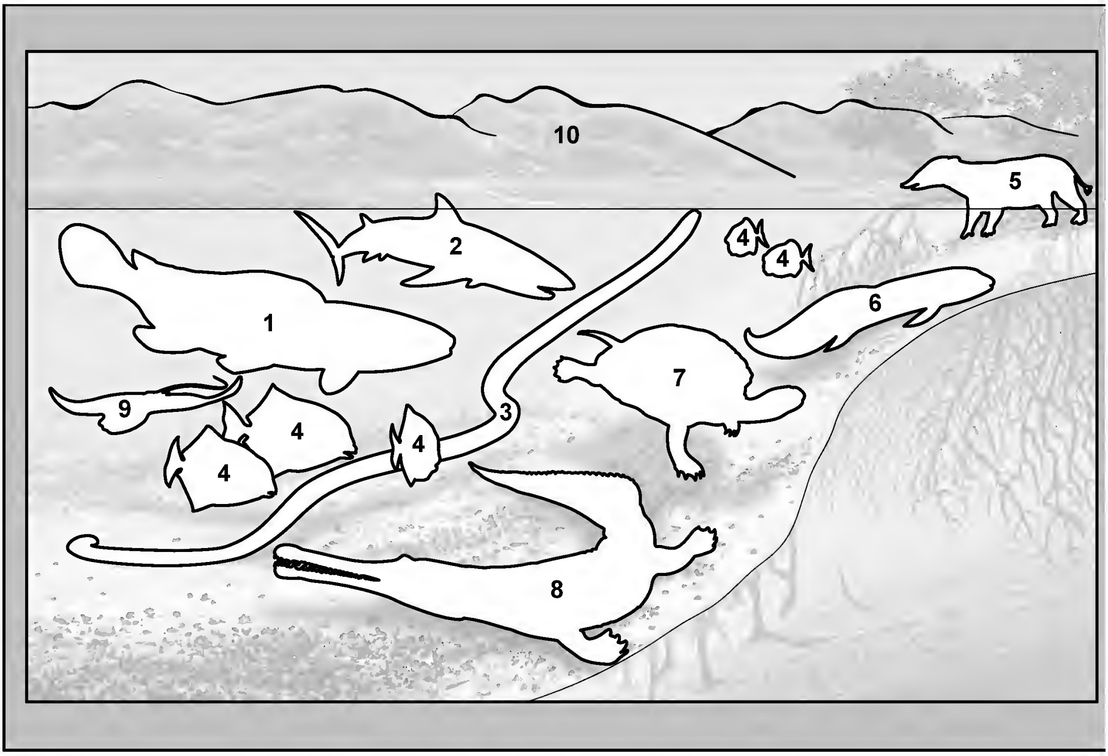
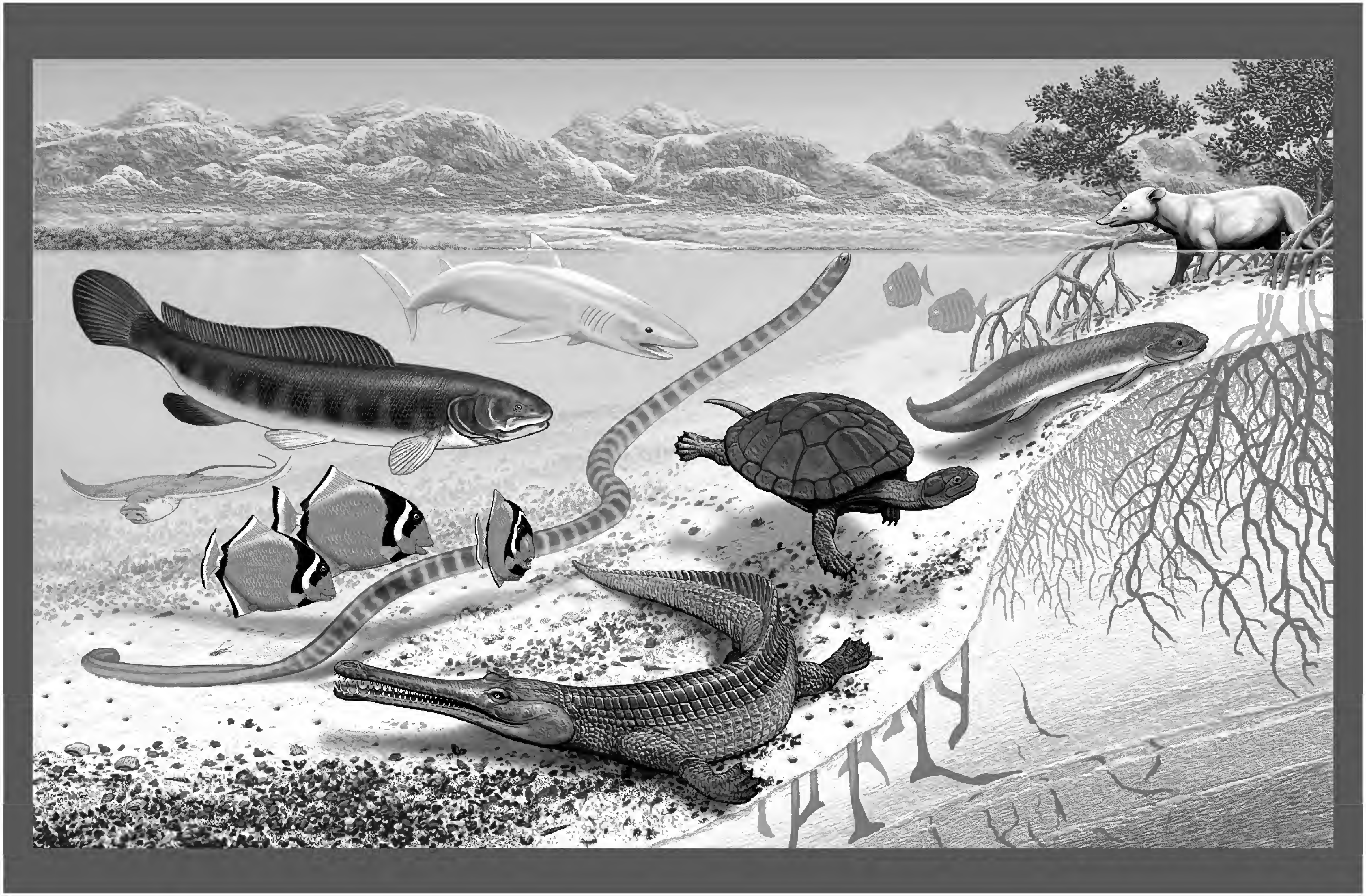


1- *Maliamia gigas*	**6-** *Lavocatodus giganteus*
2- *Cretalamna* (*Serratolamna*) *maroccana*	**7-** *Acleistochelys maliensis*
3- *Palaeophis colossaeus*	**8-** *Rhabdognathus aslerensis*
4- *Pycnodus jonesae*	**9-** *Myliobatis wurnoensis*
5- Plesielephantiform mammal	**10-** Adrar des Iforas massif

FRONTISPIECE. Reconstruction of the Trans-Saharan Seaway waters (*opposite page, foldout; with key above*) from the Late Cretaceous–early Paleogene by Carl Buell. Sunlight of the tropics illuminated seawater filled with mangrove roots near shore where freshwater influence was highest. Mollusks lined the floor of the shallow sea, and tube-shaped burrows opened onto the seafloor.



CONTENTS

ABSTRACT

An epicontinental sea bisected West Africa periodically from the Late Cretaceous to the early Eocene, in dramatic contrast to the current Sahara Desert that dominates the same region today. Known as the Trans-Saharan Seaway, this warm and shallow ocean was a manifestation of globally elevated sea level associated with the rapid break-up of the supercontinent Gondwana in the late Mesozoic. Although it varied in size through time, the Trans-Saharan Seaway is estimated to have covered as much as 3000 km^2 of the African continent and was approximately 50 m deep. The edges of the sea were defined in part by the high topography of the Precambrian cratons and mobile belts of West Africa. Over its approximately 50 million year episodic existence, through six major periods of transgression and regression, the Trans-Saharan Seaway left behind extensive nearshore marine sedimentary strata with abundant fossils. The waters that yielded these deposits supported and preserved the remains of numerous vertebrate, invertebrate, plant, and microbial species that are now extinct. These species document a regional picture of ancient tropical life that spanned two major Earth events: the Cretaceous-Paleogene (K-Pg) boundary and the Paleocene-Eocene Thermal Maximum (PETM). Whereas extensive epeiric seas flooded the interior portions of most continents during these intervals, the emerging multicontinental narrative has often overlooked the Trans-Saharan Seaway, in part because fundamental research, including the naming of geological formations and the primary description and analysis of fossil species, remained to be done. We provide such synthesis here based on two decades of fieldwork and analyses of sedimentary deposits in the Republic of Mali. Northern parts of the Republic of Mali today include some of the farthest inland reaches of the ancient sea.

We bring together and expand on our prior geological and paleontological publications and provide new information on ancient sedimentary rocks and fossils that document paleoequatorial life of the past. Ours is the first formal description of and nomenclature for the Upper Cretaceous and lower Paleogene geological formations of this region and we tie these names to regional correlations over multiple modern territorial boundaries. The ancient seaway left intriguing and previously unclassified phosphate deposits that, quite possibly, represent the most extensive vertebrate macrofossil bone beds known from anywhere on Earth. These bone beds, and the paper shales and carbonates associated with them, have preserved a diverse assemblage of fossils, including a variety of new species of invertebrates and vertebrates, rare mammals, and trace fossils. The shallow marine waters included a wide range of paleoenvironments from delta systems, to hypersaline embayments, protected lagoons, and carbonate shoals.

Our overarching goal has been to collect vertebrate fossils tied to a K-Pg stratigraphic section in Africa. We provide such a section and, consistent with prior ideas, indicate that there is a gap in sedimentation in Malian rocks in the earliest Paleocene, an unconformity also proposed elsewhere in West Africa. Our phylogenetic analyses of several vertebrate clades across the K-Pg boundary have clarified clade-by-clade species-level survivorship and range extensions for multiple taxa. Few macrofossil species from the Trans-Saharan Seaway show conspicuous change at either the K-Pg boundary or the PETM based on current evidence, although results are very preliminary. Building on our earlier report of the first record of rock-boring bivalves from the Paleocene of West Africa, we further describe here a Cretaceous and Paleogene mollusk fauna dominated by taxa characteristic of the modern tropics. Among the newly discovered fossil osteichthyans, large body size characterizes both the pycnodonts and a new freshwater Eocene catfish species, one of the largest fossil catfishes found in Africa. Our new paleoecological and faunal reconstructions show an evergreen, broadleaf forest that included some of the oldest mangroves known. The ancient Malian ecosystem had numerous apex predators including Crocodyliformes, Serpentes, and Amiidae, some of which were among the largest species in their clades. The Trans-Saharan Seaway exhibited intermittent isolation from major seas. This environmental variable may have created aquatic centers of endemism, stimulating selection for gigantism as previously observed for species on terrestrial islands.

INTRODUCTION AND PRIOR RESEARCH

The Republic of Mali has extensive sedimentary deposits left by an ancient epeiric sea known as the Trans-Saharan Seaway. Based on geological and paleontological field data we collected on expeditions in northern Mali in 1999, 2003, and 2009 (the latter cut short for security reasons), we conducted two decades of analysis resulting in more than 10 publications that describe new discoveries and interpretations of the sedimentology, sequence stratigraphy, and paleobiology of this region of the Sahara (Bamford et al., 2002; Brochu et al., 2002; O'Leary et al., 2004a; Tapanila et al., 2004; O'Leary et al., 2006; Gaffney et al., 2007; Hill et al., 2008; Tapanila et al., 2008; Claeson et al., 2010; Hill et al., 2015; McCartney et al., 2018). We present here an integrated picture of that work.

An overarching goal of this field-based project was to improve the stratigraphic and phylogenetic record of species change across the Cretaceous-Paleogene (K-Pg) boundary by building a vertebrate-fossil-yielding stratigraphic section in Africa. The K-Pg boundary is the geological representation of one of Earth's five major extinction events, which brought about the elimination of an estimated 65% of vertebrate species (Archibald, 1994; Novacek, 1999; Levin, 2003). Subsequent to the K-Pg boundary, placental mammal fossils appear in the stratigraphic record for the first time (Novacek, 1999; O'Leary et al., 2004b; Wible et al., 2007; O'Leary et al., 2013). Scholars examining how the K-Pg event unfolded on a global scale have repeatedly emphasized the importance of having multiple, high-quality, stratigraphic sections—with vertebrate fossils—dispersed worldwide to test theories of extinction (Archibald, 1996; Kiessling and Claeys, 2002). Nonetheless, as discussed by Archibald (1994), only eastern Montana's Hell Creek Formation in the Western Interior of North America captures high-resolution vertebrate faunal change through this interval, making a search for new sections a high priority. Likewise, for the Paleocene-Eocene Thermal Maximum (PETM; Kennett and Stott, 1991), detailed sections with macrofossils spanning this boundary are not well represented on continental Africa. This acute (80,000–100,000 year) warming spike, thought to have resulted from perturbation of the carbon cycle, marked one of the hottest times in the Cenozoic (Röhl et al., 2007; Giusberti et al., 2016). An important interval in Earth history for climate study, the PETM is characterized by terrestrial and marine biotic change, including extinction, dispersal, and transient diversification that have been tied to global warming and ocean acidification (Kennett and Stott, 1991; Thomas and Shackleton, 1996; Speijer and Morsi, 2002; Speijer and Wagner, 2002; Schmitz and Pujalte, 2007; Sluijs et al., 2007; Jaramillo et al., 2010; McInerney and Wing, 2011).

The rocks of northern Mali offer the possibility of studying both these faunal transitions in Africa because from the Late Cretaceous to the early Paleogene the region was repeatedly crossed

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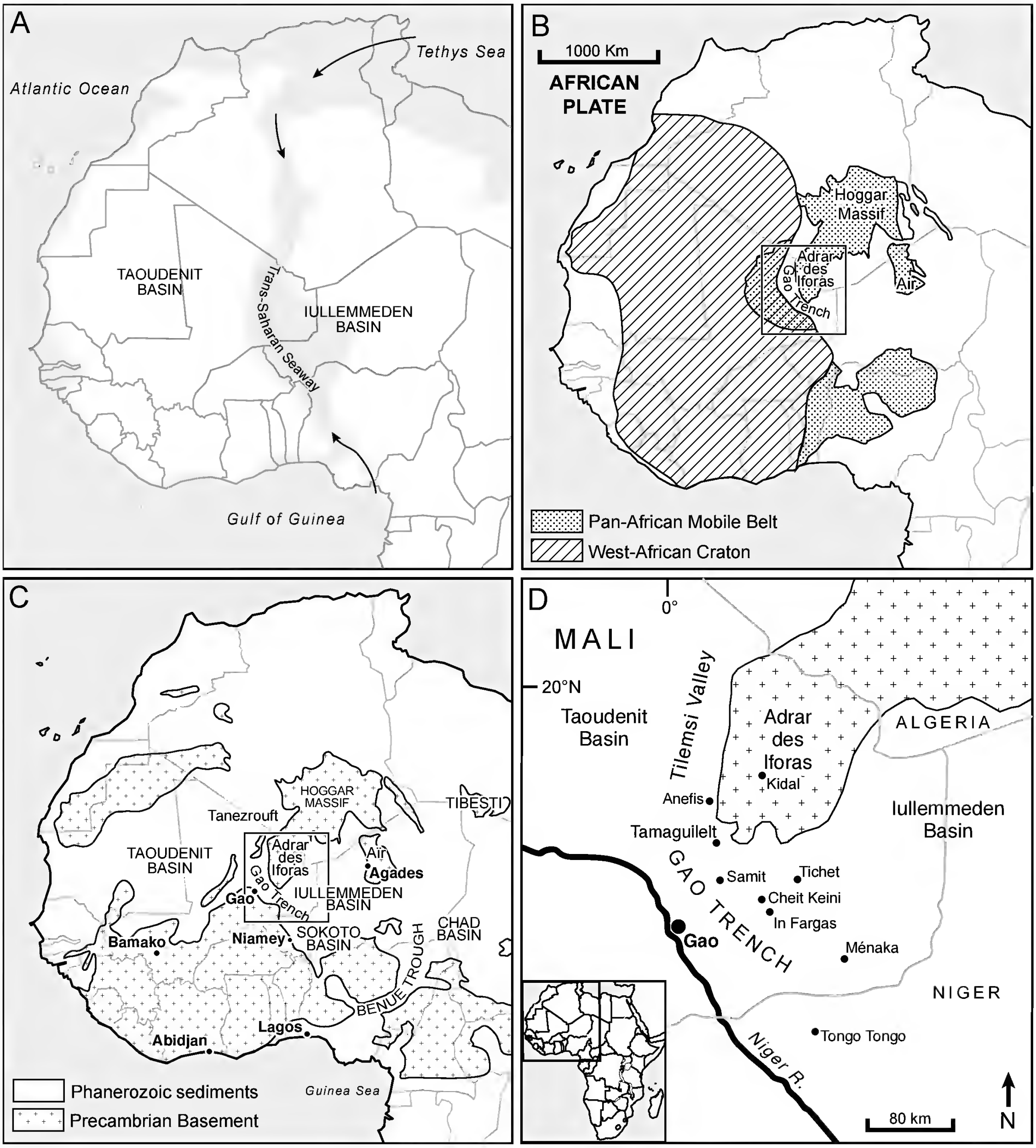
FIGURE 1. The Trans-Saharan Seaway and tectonic and geographic features in West Africa defining the field area. **A.** Generalized reconstruction of the Trans-Saharan Seaway in the Paleocene (after Kogbe, 1976); note the submerged African coastline; **B.** Tectonic features, after Black et al. (1979), Bronner et al. (1980) and Guiraud et al. (2005). Mali is on the African Plate; our field area in Mali (box) is on the West African Craton; the younger Pan-African Mobile Belt is sutured to the eastern margin of the craton. Early Cretaceous rifting resulted in the formation of the Gao Trench (a graben that may be a half graben in places) bounded by normal faults (Bronner et al., 1980; Guiraud et al., 2005; Ye et al., 2017). **C.** (after Guiraud et al., 2005: fig. 3) The three connected fossiliferous sedimentary basins investigated by us: the Taoudenit and Iullemmeden basins and the Gao Trench. The Adrar des Iforas, a Precambrian massif, was likely a major source of siliciclastic sedimentation for these basins. The adjacent Benue Trough was a low-lying conduit to the south for marine invasions into the Sokoto and Chad basins (both outside our field area). **D.** The Tilemsi Valley, a geographic depression at the eastern edge of the Taoudenit Basin, and smaller towns close to the field localities. Additional sources for these maps (Petters, 1977; Pascal and Traore, 1989; Lefranc and Guiraud, 1990).


A
Tethys Sea
Atlantic Ocean
TAOUDENIT BASIN
Trans-Saharan Seaway
IULLEMMEDEN BASIN
Gulf of Guinea
B
1000 Km
AFRICAN PLATE
Hoggar Massif
Adrar des Iforas
Gao Trench
Air
Pan-African Mobile Belt
West-African Craton
C
HOGGAR MASSIF
Tanezrouft
TIBESTI
TAOUDENIT BASIN
Adrar des Iforas
Air
Agades
Gao
Gao Trench
IULLEMMEDEN BASIN
Bamako
Niamey
SOKOTO BASIN
BENUE TROUGH
CHAD BASIN
Abidjan
Lagos
Guinea Sea
Phanerozoic sediments
Precambrian Basement
D
0°
MALI
20°N
Taoudenit Basin
Tilemsi Valley
Adrar des Iforas
Kidal
ALGERIA
Anefis
Iullemmeden Basin
Tamaguilelt
GAO TRENCH
Samit
Tichet
Cheit Keini
In Fargas
Gao
Ménaka
NIGER
Tongo Tongo
Niger R.
80 km
N

by a body of ocean water known as the Trans-Saharan Seaway. The Trans-Saharan Seaway (fig. 1A) was an offshoot of the Tethys Sea, the latter having formed between Laurasia and Gondwana during the Mesozoic Era as the supercontinent Gondwana fragmented (Berggren, 1974; Axelrod and Raven, 1978). During the Late Cretaceous and early Paleogene, when global temperatures were relatively high and sea levels were elevated due to tectonic and other influences, numerous epeiric (epicontinental) seas like the Trans-Saharan Seaway developed periodically and in several locations worldwide (Huber et al., 2002; Miller et al., 2005; Swezey, 2009: 89; Haq, 2014).

The sedimentary rocks of Mali preserve the passage of this ancient sea into three major depocenters (basins) of West Africa: the Taoudenit Basin, the Gao Trench and the Iullemmeden Basin. These strata are exposed along the margins of elevated Precambrian basement rocks known as the Adrar des Iforas massif (fig. 1B, C), and study of this sedimentary environment and its fossils has been underway for over a century (Lapparent, 1905; Kilian, 1931; Furon, 1935; Cornet, 1943; Radier, 1959; Krasheninnikov and Trofimov, 1969; Berggren, 1974; Adeleye, 1975; Kogbe et al., 1976; Petters, 1977; 1979; Reyment, 1979; 1980; Bassot et al., 1981; Boudouresque et al., 1982; Reyment and Schöbel, 1983; Reyment, 1986; Bellion et al., 1989; Pascal and Traore, 1989; Bellion et al., 1990; Lang et al., 1990; Moody and Sutcliffe, 1990; Damotte, 1991; Moody and Sutcliffe, 1991; Mateer et al., 1992; Moody and Sutcliffe, 1993; Ratcliffe and Moody, 1993; Tintant et al., 2001; Swezey, 2009). Early reports of fossil marine invertebrates collected far from modern coastlines in Mali's Tilemsi Valley (fig. 1D) were described as similar to fossil species in Algeria and Libya, and suggested to investigators both the presence of ancient seas and a past connection of those seas to the Atlantic (Lapparent, 1905). Using a combination of biostratigraphy and the relative positions of sedimentary formations (no volcanic sediments are found in the area) the scientists mentioned above dated the regional rocks as Upper Cretaceous through Eocene in age. Initially, fossil discoveries tended to be reported only briefly in the context of geological work (e.g., Lavocat, 1953; Lavocat and Radier, 1953; Radier, 1959; Tabaste, 1963; Rage, 1983), but following British expeditions of the 1980s more specialized taxonomic treatments began to emerge (e.g., Longbottom, 1984; Patterson and Longbottom, 1989; Longbottom, 2010).

Despite these important contributions to geological mapping, stratigraphy, and paleontology, prior to our work, the rocks in this region of Mali had yet to be described using formal stratigraphic nomenclature even though they had been studied for much of the 20th century. Early reports followed standard lithostratigraphic and biostratigraphic approaches (e.g., Radier, 1959; Greigert, 1966; Bellion et al., 1989), and the broad dynamics of the observed sedimentary cycles were articulated by Petters (1977) based on translations of the findings of Russian scientists Krasheninnikov and Trofimov (1969). Efforts to map the changing geography of the Trans-Saharan Seaway waters through time required the integration of numerous field observations by hand (e.g., Adeleye, 1975; Kogbe et al., 1976; Petters, 1977; 1979; Reyment, 1979; 1980; Kogbe, 1981; Boudouresque et al., 1982; Adetunji and Kogbe, 1986; Reyment and Dingle, 1987; Bellion et al., 1989; Kogbe, 1991; Damotte, 1991; 1995). Reyment (1980) estimated that, when completely connected, the Trans-Saharan Seaway covered as much as 2500–3000 km^2.

We have additionally incorporated sequence stratigraphy to improve or resolve age relationships and regional correlations, such as the frequency of early Paleogene sea-level cyclicity in Mali and relationships to previously described deposits in Nigeria (Dikouma et al., 1993). Using our new correlated stratigraphic sections, we have developed revised and computer-modeled paleogeographic maps of this vast inland sea. As we demonstrate herein, our new field data allow us to address more precisely when the Tethys Sea and the South Atlantic were fully connected.

Gaining a global picture of major transitions in Earth history like the K-Pg or PETM requires taking fossil discoveries one step further by integrating alpha taxonomy, stratigraphy, and phylogenetics. We have consistently tried to provide such analysis for our Trans-Saharan Seaway fossil discoveries (Brochu et al., 2002; O'Leary et al., 2004a; Gaffney et al., 2007; Hill et al., 2008; Claeson et al., 2010). As we discuss below, the paleoecology of the Trans-Saharan Seaway was that of a shallow marine ecosystem with nearshore mangroves and offshore water averaging approximately 50 m deep (Krasheninnikov and Trofimov, 1969; Berggren, 1974). The fossil mangroves are among the oldest records of these angiosperms, which are hypothesized to have first appeared in the Late Cretaceous in several locations along the margin of the Tethys Sea (Ellison et al., 1999). Drawing on our findings, and as part of this synthesis, we provide graphical reconstructions of the paleoecosystems that existed during the sea's transgressive-regressive events and the animals and plants that inhabited it.

Our field area is noteworthy for being located in a part of the world that presents extreme physical challenges due to the severe environment of the Sahara Desert (Novacek, 2008). In addition, security challenges exist on the relatively open international border of northern Mali that required the team to collaborate with the Malian military (appendix 1). As we write this monograph, scientific fieldwork in the northern areas of the Republic of Mali has ceased due to entrenched conflict and political instability (Fowler, 2011; Cristiani and Fabiani, 2013; Dowd and Raleigh, 2013; Francis, 2013). This conflict tragically affects both the Malian authors of this paper and the people in the region where this fieldwork occurs. As it is unclear when scientific activities might resume, it is timely to synthesize what we have accomplished to date.

Epeiric Seas: Definitions and Modern Comparisons

Epeiric seas are shallow bodies of ocean water that have flooded onto continental crust, potentially extending for thousands of kilometers inland while often retaining connections to a larger open ocean. Such seas, which are very broad and shallow (<200 m deep) by comparison to deep oceanic basins (closer to 5000 m deep), may also have substantial freshwater influence (Menard and Smith, 1966; Schlager, 2005). The Trans-Saharan Seaway (fig. 1A) was one of several intracratonic seaways that existed globally during the late Mesozoic and early Cenozoic (Haq et al., 1987). It bisected West Africa and created temporary unions between the Tethys Ocean, entering West Africa from the north, and the Gulf of Guinea, entering from the south (Adeleye, 1975; Reyment, 1980; Kogbe, 1981; Bellion et al., 1990). Sediments deposited by epeiric seas represent some of the best-preserved marine rocks on Earth for the study of paleontology and geologic processes because by being internal to continents they are more removed from destructive tectonic events that could eliminate them (Harries, 2009).

A few modern examples of epeiric seas do exist. The Caspian Sea is a landlocked remnant of the ancient Tethys Ocean (Zonenshain and Pichon, 1986), and the Baltic Sea is another small, inland sea on continental crust where fresh and seawater mix (Winterhalter et al., 1981). The Hudson Bay in Canada is also flooded continental crust, and thus an epeiric sea, but not one on the scale of the Trans-Saharan Seaway (Harries, 2009). Closer to the tropics, the Java Sea, which is surrounded by the islands of Indonesia, is perhaps the best modern analog of a tropical epeiric system (Tjia, 1980). The phenomenon of ancient shallow seas can be particularly striking for its contrast to the modern environment occupying the same geographic location. The area once covered by, and supporting life within, the Trans-Saharan Seaway is now occupied by the Sahara, the world's largest hot desert (Tucker et al., 1991).

The characteristics of shallow marine ecosystems and shelf seas provide an imperfect analog for interpreting the Trans-Saharan Seaway (Harries, 2009). Coastlines can be defined as the "intertidal and subtidal areas on and above the continental shelf (depth of 200 m); areas routinely inundated by saltwater; and adjacent land, within 100 km from the shoreline" (Martinez et al., 2007: 256). The ocean covering of modern continental shelves is typically only 70 km inland, with an average water depth of 133 m, and rarely exceeds 200 m deep (Tyson and Pearson, 1991; Bianconi, 2002). Such shallow ocean covering of continents tends to consist of waters that are well mixed by seasonal winds, which influences the chemistry of the waters (Tyson and Pearson, 1991). Such waters are also impacted by tides and are categorized as part of the neritic zone of the ocean (Bianconi, 2002; James and Jones, 2016). Modern ocean coverage on continental crust constitutes some of the most biologically rich ocean regions, with the exception of hydrothermal vents (Bianconi, 2002; Martinez et al., 2007).

Tectonics, Geography, and Eustasy Impacting the Trans-Saharan Seaway

Tectonic Factors Shaping Geography. Large-scale tectonic activities and Precambrian basement geology in West Africa inform our understanding of why the fossiliferous sedimentary deposits of Mali were deposited where they are. Tectonics are also a major variable controlling sea-level change, defining crustal boundaries and zones of weakness that created low-relief basins. Such basins can receive water as well as sediment infill from the weathering of high-relief Precambrian massifs. During the time of the Trans-Saharan Seaway, three major variables contributed to high sea level and continental inundation. Rapid sea-floor spreading created younger, hotter, and more buoyant oceanic lithosphere, which displaced seawater onto continental crust. Secondly, a lack of continental ice sheets meant more water was in circulation globally, and third, low topography of continents due to tectonic subsidence provided areas for inland seas to collect (Harries, 2009).

Our field localities, and the entire country of Mali, are situated on the African Plate (fig. 1B), which consists of both oceanic and continental crust. Spreading at the African Plate's divergent boundary with the North American Plate as part of the fragmentation of Gondwanaland, brought about the opening of the southern Atlantic Ocean in the late Mesozoic (Burke, 1996). Such crustal movement was consequential for shaping the low-lying basins in West Africa (Guiraud et al., 2005). A part of the African Plate that has been stable for over 2 billion years is the Proterozoic West African Craton, which has a north-south orientation and underlies much of West Africa, including western Mali (fig. 1B; Black and Liegeois, 1993; Guiraud et al., 2005). The eastern border of the West African Craton is sutured to the Pan-African Mobile Belt (alternatively called the Trans-Saharan Belt or Pharusian Belt), an ancient orogenic mobile belt that represents an upwardly folded segment of Earth's continental crust. This belt was produced during the Pan-African orogeny, a Precambrian mountain-building event related to the formation of the Gondwanan supercontinent (Black and Liegeois, 1993; Guiraud et al., 2005: figs. 5, 8). Pan-African orogeny structures that form modern geographic landmarks in our field area include the Adrar des Iforas Precambrian massif, a geographic elevation composed of Precambrian crystalline basement rocks that likely provided sediment supply for surrounding basins (Petters, 1979: fig. 1A).

Recent tectonic plate reconstructions indicate that movement and counterclockwise rotation of the African continent positioned Mali and the rest of West Africa within the equatorial region, between 7°–15° north latitude, from the Late Cretaceous to the middle Eocene, and simultaneously opened a broad Tethyan Ocean to the north (Heine et al., 2013; Matthews et al., 2016; Müller et al., 2016; Ye et al., 2017). Across West Africa several large intracratonic basins, including the Iullemmeden, Taoudenit, and Chad basins, were affected by major Gondwanan break-up events (Petters, 1979: fig. 2B). These long-lived intracratonic basins originally formed due to failed rifting and their shape has been modified by the periodic reactivation of far-field stresses, sag-basin development and compressional tectonics associated with changes in plate motions (Guiraud et al., 2005). Thus, these basins experienced lithospheric attenuation and subsidence during major phases of continental breakup. As they subsided, they became conduits and reservoirs for the Trans-Saharan Sea to infill when it moved onto the West African Craton (fig. 1A–C).

Another determining factor in the geographic position of sedimentary beds was the formation in the Early Cretaceous of the Gao Trench, an event linked to the development of the Central African Rift System during the opening of the South Atlantic (Guiraud et al., 2005). The Gao Trench (fig. 1) is a narrow, east-west trending graben (and may be a half graben in places) that connects the Taoudenit and Iullemmeden basins. The part of the Trans-Saharan Seaway that specifically infilled the Gao Trench between the Late Cretaceous and Eocene has been referred to as the Détroit Soudanais (Radier, 1959). Although not connected to other segments of the Central African Rift Zone, the Gao Trench region holds a deep (>1 km) Cretaceous-Paleogene stratigraphic succession that records epeiric sea sedimentation from water that flowed between the Taoudenit and Iullemmeden basins.

Our research has concentrated on the Gao Trench and the parts of the Iullemmeden and Taoudenit basins that extend into Mali, areas that were in the Late Cretaceous–early Paleogene, and are today, thousands of kilometers from the open ocean (fig. 1). Given the inland location of these areas, the sedimentary rocks now found there were, as we noted above, deposited in reactivated basins undergoing extensional tectonics linked to far-field stresses associated with the breakup of Gondwana (Guiraud et al., 2005: fig. 1b). The 800,000 km^2 Iullemmeden Basin (fig. 1C, D) extends through modern Algeria, Nigeria, Benin, Chad, Niger, and Mali, where it occupies most of the country east and southeast of the Adrar des Iforas Precambrian massif (Kogbe, 1981; Bellion et al., 1989; Moody and Sutcliffe, 1991; Zaborski and Morris, 1999). The basin has a gentle syncline shape and sedimentary deposits of the Trans-Saharan Seaway collected widely within it due to its low elevation (Radier, 1959; Boudouresque et al., 1982; Kogbe, 1991). The Taoudenit Basin is an even more extensive (2 million km^2) structural feature of the West African Craton that comprises the greater part of northern Mali (Bronner et al., 1980; Bassot et al., 1981). Upper Cretaceous–Eocene Trans-Saharan Seaway strata in the syncline known as the Tilemsi Valley (Bellion et al., 1989) are best ascribed to the Taoudenit Basin because they overlie the deformed Pan-African Mobile Belt that defines the eastern boundary of that basin (Guiraud et al., 2005: fig. 5). The more southerly Benue Trough, which is not in Mali but is relevant when discussing the regional continental flooding, also formed as the product of rifting in the Early Cretaceous (Guiraud et al., 2005).

EUSTASY AND SEDIMENTARY ROCK FORMATION. Tectonic factors induced marine incursions onto West Africa as early as the Aptian-Albian approximately 113 million years ago (Moody and Sutcliffe, 1993). Those transgressions are, however, distinct from the Late Cretaceous ones that started in the Cenomanian-Turonian, which are the focus of our research. An increased rate of sea-floor spreading at mid-ocean ridges, not only in the Atlantic, but globally, was underway in the Late Mesozoic (Hays and Pitman III, 1973; Reyment and Dingle, 1987; Miller et al., 2005). This type of lithospheric activity increases the volume of midocean ridges and adjacent crust due to thermal expansion of sea-floor rocks. As a result, there is less volumetric capacity in the ocean basins, which forces ocean water onto land where it finds its way to low-relief areas. Pulses of ridge growth and the accumulation of newer, hotter lithosphere have been tied to transgressions, whereas intervening periods of suspended growth are linked with regressions (Hays and Pitman III, 1973).

The subject of our work is the series of transgressive cycles that started in the Cenomanian and continued through the middle Eocene, leaving extensive sedimentary deposits in Mali. These strata comprise mixed carbonate deposits generated in situ along with siliciclastic deposits weath-

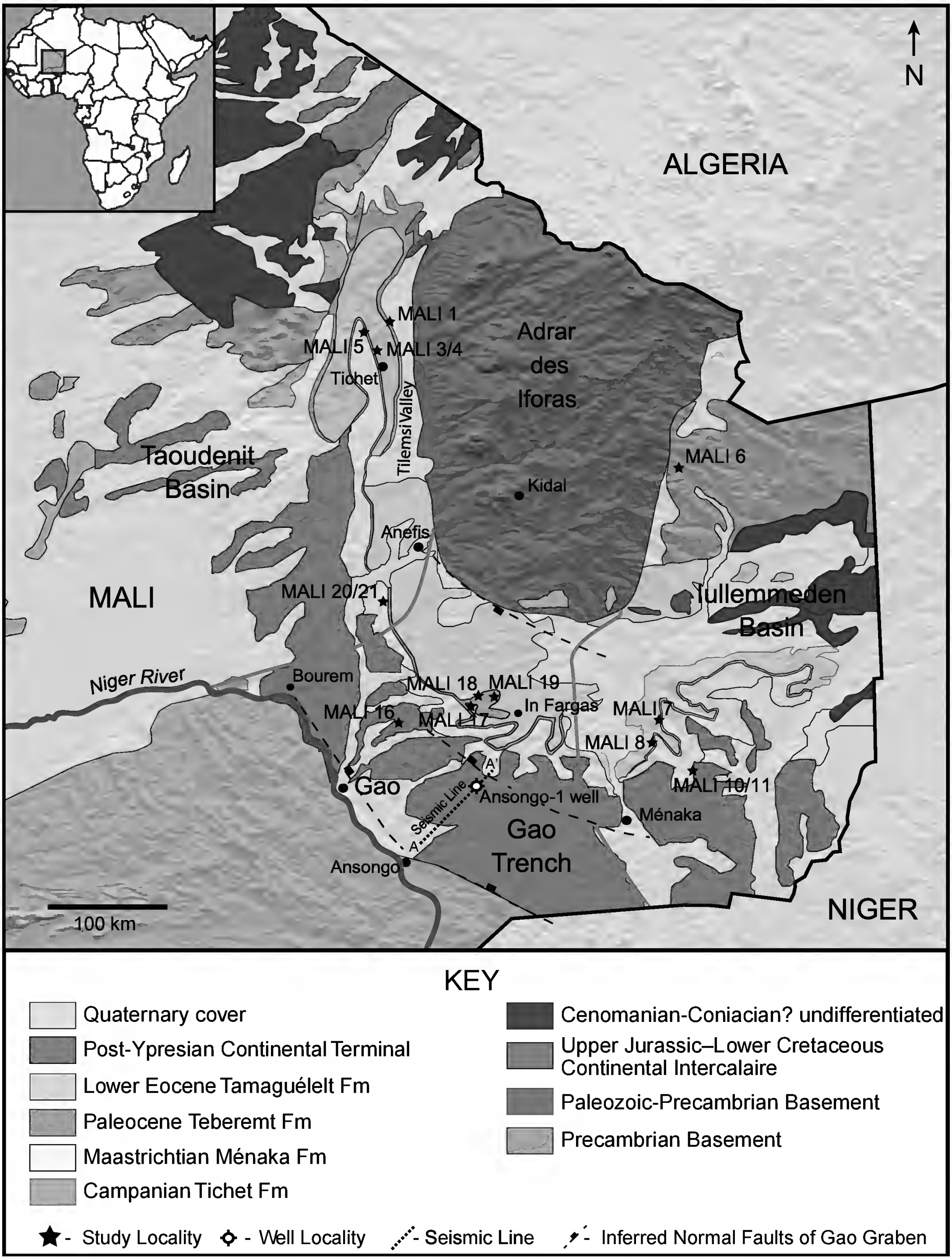


FIGURE 2. Map of northwestern Mali with our localities from the 1999 and 2003 expeditions plotted on a topographic map with exposed geologic formations indicated. The location of the "Ansongo-1" well log (appendix 2) is also indicated (Elf-Aquitaine, 1979). Note the restricted exposure of the Paleocene Teberemt Formation. Gao Trench graben margins indicated by dashed lines. Orange lines demarcate three major depocenters.

ered from the Adrar des Iforas massif, all of which settled into the Iullemmeden and Taoudenit basins and the Gao Trench (Petters, 1979; Reyment and Dingle, 1987; Tapanila et al., 2004; Tapanila et al., 2008). The resulting sedimentary units are relatively thin and lie unconformably on one of the following: pre-Cenomanian continental sediments, Jurassic or Cambrian-Permian strata, or, in some cases of maximum transgression, directly on the Precambrian basement strata of the Adrar des Iforas massif (Radier, 1959; Reyment, 1980; Moody and Sutcliffe, 1991; 1993; Tapanila et al., 2004; Tapanila et al., 2008)

At high sea level, the southern embayment of the Tethys Ocean extended inland along the coast of North Africa and the Trans-Saharan Seaway specifically was its north-south trending arm that reached into Libya, Algeria, Mali, Niger, and even northern Nigeria, taking different routes at different times (fig. 1A; Petters, 1977: fig. 9; Boudouresque et al., 1982: fig. 2). Our field localities in Mali are situated to the west, south, and east of the Adrar des Iforas and represent some of the most inland reaches of the ancient sea (fig. 2). In the Taoudenit Basin, Mesozoic rocks are concentrated directly along the western margin of the Adrar des Iforas in the Tilemsi Valley (fig. 2). As we noted above, the thickest succession of Trans-Saharan Seaway deposits lies to the south and east of the Tilemsi Valley in the Gao Trench. At times the Trans-Saharan Seaway mixed with ocean water that had flooded West Africa via the southerly Benue Trough and the Sokoto Basin (Kogbe et al., 1976; Petters, 1977; 1979; Adetunji and Kogbe, 1986; Reyment and Dingle, 1987).

Finally, it is helpful to contextualize how different the Late Cretaceous world was relative to the Recent. Sea level has shown a 400 m range of variation over the Phanerozoic, and extensive geological evidence indicates that it was higher in the Late Cretaceous than at any point over the last 250 my (Tyson and Pearson, 1991; Harries, 2009; Haq, 2014). In the Cretaceous, as much as 40% of current continental land was submerged under 50–100 m of ocean water (Hays and Pitman III, 1973; Miller et al., 2005). Global sea level today is approximately 300 m lower than it was during the Late Cretaceous (Campanian), and is at one of its lowest points in the last 250 my (Haq et al., 1987; Falkowski et al., 2004; Haq, 2014). By comparison, the estimate for climatically mediated sea-level change from human-generated global warming predicts, at maximum, a sea-level elevation of approximately 2 m by the end of the 21st century (NOAA, 2012). While a 2 m sea elevation would be disastrous for current populations of humans (Nicholls et al., 1999), it is noteworthy that such change differs significantly in size and mechanism from the sea-level changes of the Late Cretaceous under investigation here.

PALEOENVIRONMENT OF THE TRANS-SAHARAN SEAWAY

TEMPERATURE AND SEASONALITY. The Malian portion of the Trans-Saharan Seaway was located in the paleotropics, between paleolatitudes 23° 27′ north and south of the equator (Matthews et al., 2016, and references therein), thus geographic position alone suggests that the Trans-Saharan Seaway would have been relatively warm (fig. 1; see also GPlates Reconstruction of the Trans-Saharan Seaway, below). The same tectonic activity described above affecting sea level is also hypothesized to have caused a greenhouse climate in the Late Cretaceous–early Paleogene due to the release of carbon dioxide (Hallam, 1985; Kennett and Stott, 1991; Pearson et al., 2001; Shellito et al., 2003; James and Jones, 2016). Evidence for this hypothesis comes from the study of fossil foraminiferan tests that contain oxygen isotopes that vary depending on the temperature of the water in which the shells formed (Urey, 1947; Pearson et al., 2001; Zachos et al., 2001). Coupled with deep-sea drilling projects that sample such temperature proxies on a large scale, a picture of a Late Cretaceous–early Paleogene "hothouse" interval has emerged (Savin, 1977; Kennett and Stott, 1991), a time when Earth probably lacked polar ice sheets (Markwick, 1998; Pearson et al., 2001; Zachos et al., 2001; Royer, 2006).

In the late Mesozoic, the sea surface temperature of water in the tropics may have been as high as 33°–34° C (Norris et al., 2002) and on the northern part of the African continent the temperature may have averaged ~30°–36° C (Sellwood and Valdes, 2006). The very presence of enormous bodies of sea water on continents, like the Trans-Saharan Seaway, also is thought to have stabilized global heat and spread it broadly as heat is very effectively stored and transported in water (Hays and Pitman III, 1973; Harries, 2009). Bioproxies for temperature, such as body size in South American fossil snakes and the physiological limitations it imposes, have been used to suggest that the paleotropics may have been even hotter than the present-day tropics (Pearson et al., 2001; Head et al., 2009). Our discovery of relatively large extinct snakes in Mali is another body-size data point suggesting that the African paleotropics in and around the Trans-Saharan Seaway may also have been relatively hot (McCartney et al., 2018).

Modern tropical climates typically lack strong seasonal temperature change and frost (Linacre and Geerts, 2002), characteristics that would have likely described the Trans-Saharan Seaway. An isotopic study of the shell composition of tropical Cretaceous bivalves indicated that seasonal fluctuations in temperature were of relatively low amplitude during the warmer parts of the Cretaceous, such as the Campanian through the Maastrichtian (Steuber et al., 2005). Markwick (1998) also emphasized that the presence of ancient dyrosaurid crocodyliforms in Mali is consistent with the Trans-Saharan Seaway having had a mean annual temperature no colder than 14.2° C.

Important for the time interval under study here is also the occurrence of extreme temperature changes over short durations. A spike in global temperature known as the Paleocene-Eocene Thermal Maximum (PETM) occurred 56 my ago, and was globally among the hottest times of the last 250 million years (Kennett and Stott, 1991; Thomas and Shackleton, 1996; Zachos et al., 2001; Zachos et al., 2008; McInerney and Wing, 2011). During the PETM, climate warmed an estimated average of 5° C over only ~5 ky, a relatively short interval geologically (Zeebe et al., 2016; Kirtland Turner et al., 2017; Kirtland Turner, 2018), and then cooled to preevent levels over only ~100 ky (Kennett and Stott, 1991). The PETM has been associated with terrestrial faunal change in North America (Wing et al., 2005; Woodburne et al., 2009), but is only beginning to be investigated in continental African rocks.

PRECIPITATION AND COMPOSITION OF WATER: Modern tropical climates often exhibit profound seasonal variation in precipitation and this also may have been the case for the Trans-Saharan Seaway. Hallam (1985: fig. 8), however, specifically reconstructed the northern region of the Trans-Saharan Seaway as lying within an arid belt and the more southerly part as ranging from seasonally wet to consistently wet. He presented ideas that reinforced interpretations of Petters (1977), who argued that, as in the modern Red Sea, there was little circulation in the water of the Trans-Saharan Seaway and the environment was arid. Adetunji and Kogbe (1986), however, based on their studies in the Maastrichtian Dukamaje Formation of the Nigerian part of the Trans-Saharan Seaway, argued instead for significant water circulation. The model of Sellwood and Valdes (2006) also indicated that the Late Cretaceous had humidity that varied with seasons and precipitation that exceeded evaporation. When sea level was high, such as during the interval under study here, oxygen-deficient ocean waters may have been relatively common (Tyson and Pearson, 1991). Tethyan marginal sediments in particular are hypothesized to have been dysoxic at the PETM (Speijer and Wagner, 2002). The fauna we describe below can be considered brackish to normal marine. Intermittent downpours of rain may have periodically and dramatically decreased the salinity of the Trans-Saharan Seaway, quickly killing stenohaline species (Reyment and Dingle, 1987: 105).

The opposite condition, hypersalinity, of the Trans-Saharan Seaway has also been proposed, a condition that would be linked to periods of aridity (Reyment, 1980). The widespread existence of shallow seas is hypothesized as having caused a substantial increase in seawater evaporation and the creation of highly saline ocean bottom waters in general (Brass et al., 1982). In Mali, gypsum and salt deposits occur in the very earliest part of the section we examined, the Cenomanian-Turonian sediments of the Tilemsi Valley of the Taoudenit Basin, which Reyment (1980: 317) interpreted as recording extremely arid time intervals. The late Cenomanian deposits, but not subsequent ones, were also characterized by black shales that Reyment and Dingle (1987: 102) interpreted as pockets of "stagnation." Moreover, there were quite possibly intervals during which the sea, or parts of it, was not connected to the Tethys and any embayments may have become shallow, warm and hypersaline (Petters, 1979; Reyment, 1980).

Tidal Activity: Given their broad and shallow geographic expanse, epeiric seas are thought to have been microtidal, or to have had a tidal range of approximately 2 m (James and Jones, 2016: 254). Petters (1979: 753) wrote that there are few "current-induced sedimentary structures" in the Upper Cretaceous-Paleogene rocks of the Malian region, and that the predominance of sediments with high mud content suggests that in the most internal reaches of marine embayments, the water was "low energy." As we discuss below, this generalization is not supported by our observations of the Upper Cretaceous rocks because we identified sandstones with abundant delta foresets, a signature indicative of high coastal energy. We do not see evidence of cross-laminated sandbodies, an indicator of strong currents. Thus, the generalization of Petters (1979) is a reasonable summary of the sedimentary signal in many aspects of the younger rocks of the region, except the phosphate conglomerates interleaved throughout the three younger formations, that indicate storm-related winnowing activity and persistent fair-weather wave action during deposition (Tapanila et al., 2008). Thus, fair weather and storm waves would have been the major means by which the Trans-Saharan Seaway water mixed (James and Jones, 2016). Without other forms of water mixing, stratification of the epeiric sea may have occurred, which would have limited the circulation of nutrients and possibly affected primary producers like phytoplankton.

Repository and Institutional Abbreviations

Repository: The specimens collected belong to the Republic of Mali. From 1999–2019 they have been on loan for scientific research to the laboratory of M.A. O'Leary in the Department of Anatomical Sciences, Renaissance School of Medicine, Stony Brook University, Stony Brook, New York. The specimens were originally cataloged with the prefix "CNRST-SUNY" (defined below). With permission from the Republic of Mali, the specimens are being transferred to the Department of Paleontology, American Museum of Natural History in 2019. Specimens in this paper carry the original catalog numbers and appendix 4 lists their newly assigned AMNH numbers. As of this writing the collection contains three holotypes. CT scans and other digital media associated with the paper are deposited in MorphoBank, Project 2735 (www.morphobank.org).

Abbreviations: ANSP, Academy of Natural Sciences, Philadelphia; CNRST-SUNY, joint collection of the Centre National de la Recherche Scientifique et Technologique, Bamako, Republic of Mali and Stony Brook University, Stony Brook, New York; MUVP, Mansoura University, Vertebrate Paleontology collections, Mansoura, Egypt; NHMUK PB V, paleobotany collection and PV P, R, and M, paleovertebrate collections of fish, reptiles, and mammals, Natural History Museum London; TGE, ensemble divisions for Muséum National d'Histoire Naturelle specimens from Morocco, Algeria, and/or Mali from Martin (1995). Superscripts in the Systematic Ichnology and Systematic Paleontology sections indicate locality numbers.

GEOLOGICAL RESEARCH AND ANALYSIS

Subdivision and Proposed Nomenclature for the Upper Cretaceous-Lower Paleogene Stratigraphy in Northeastern Mali

For nearly a century, geologists have recognized that Malian deposits of the Trans-Saharan Seaway have similarity to and continuity with better-studied sediments in Nigeria and Niger. As a result, gross-scale stratigraphic correlations have been proposed by many authors for Malian deposits throughout the Taoudenit and Iullemmeden basins and the Gao Trench (e.g., Radier, 1953; Krasheninnikov and Trofimov, 1969; Berggren, 1974; Petters, 1977; Bassot et al., 1981; Reyment and Schöbel, 1983; Moody and Sutcliffe, 1991; Mateer et al., 1992; Tintant et al., 2001; Swezey, 2009). The importance of these attempts at broad geographic correlation notwithstanding, such efforts have lacked precision regarding Malian rocks, and were often based on more extensive investigation of deposits in Nigeria and Niger than in Mali. As a result, such correlations have been difficult to apply on the ground in Mali because much of the prior work to date had been based on regional-scale mapping or well-logging in the Gao Trench. Aside from the seminal fieldwork by Radier (1959), little attention has focused on correlation of outcrops and stratigraphies among the three different depocenters in Mali.

Synthesis has been further complicated by a lack of formal or consistent stratigraphic nomenclature associated with the deposits in Mali. Many workers have simply referred to units in Mali by formation names described from type sections in Nigeria or Niger (e.g., Dange Formation, Wurno Formation sensu Petters, 1979) without supplying or referring to detailed lithostratigraphic descriptions for the sections in Mali. However, as our work attests, the stratigraphy and sedimentology of the deposits in Mali, while generally similar to other deposits across the Trans-Saharan Seaway region, are sufficiently different to prohibit direct correlation based on lithostratigraphic definitions alone.

The development of a formal lithostratigraphic framework for the Mesozoic-Cenozoic deposits in Mali is critical for continued progress in the correlation of strata across and within national borders. In addition, such a framework represents a foundation for studying the complexities and variations of sequence stratigraphy and paleoenvironments in the ancient seaway as a whole. Toward this end, Moody and Sutcliffe (1991, 1993) provided an initial lithostratigraphic nomenclature for the Maastrichtian-Eocene deposits in Mali. They did not, however, describe any of the units using formal type sections and boundary definitions, critical information necessary for subsequent identification of rock units as outcrops. As such, the published names and definitions of these units have minimal utility.

Using our own field-based stratigraphic work and two decades of research on the new localities we established in Mali (plate 1; table 1), we provide here formal definitions of stratigraphic units and designate type or lectostratotype sections for these rocks. Because the names proposed by Moody and Sutcliffe (1991, 1993) have found their way into the literature, we have attempted to repurpose them in our formal designations, rather than abandon the terms at risk of causing further confusion. We are aided in this effort by access to an unpublished well log, "Ansongo-1" (fig. 2; appendix 2), that provides critical new details for correlation (Elf-Aquitaine, 1979).

We propose formal subdivisions and definitions of a number of Upper Cretaceous–Paleogene sedimentary deposits exposed within and across Mali, and correlate measured sections through these units among the Iullemmeden and Taoudenit basins and the Gao Trench study areas (plate 1). Subdivision is strongly warranted based on distinctive lithological and depositional variations, as well as temporal differences among these units. Subdivision is also necessary to provide context for describing the floras and faunas from the

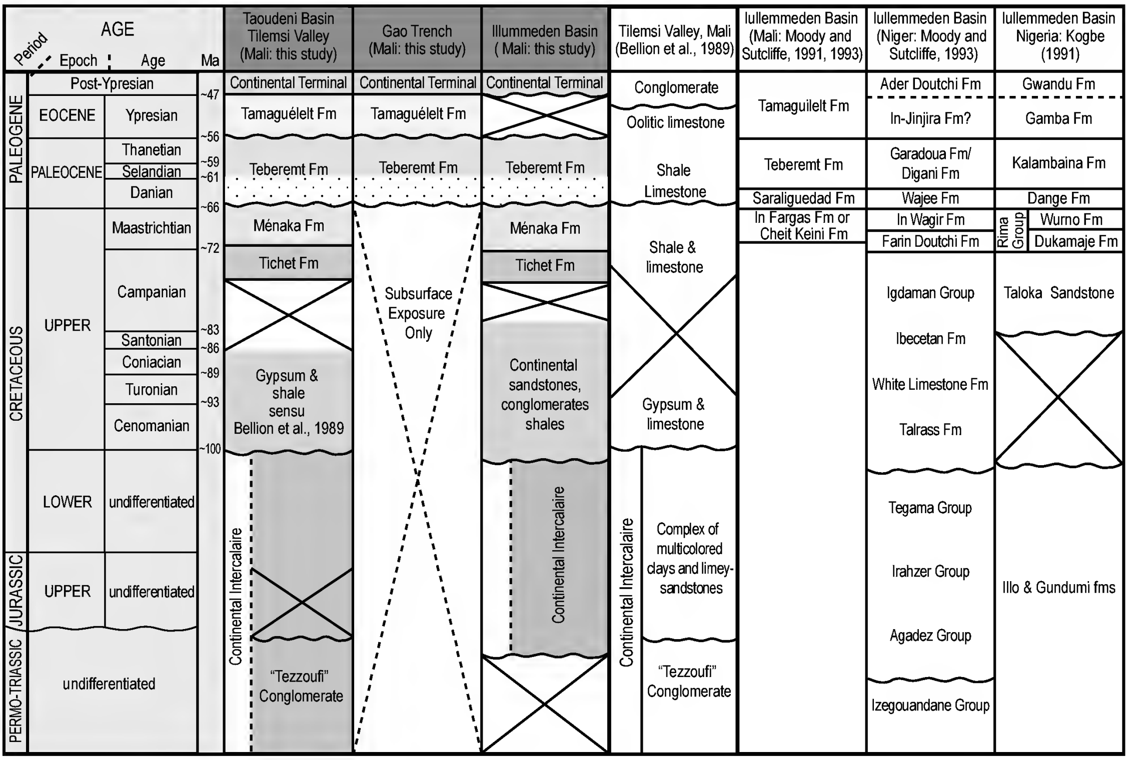


FIGURE 3. Composite of formation names, several formally diagnosed here for the first time, through the Trans-Saharan Seaway of Mali and equivalent rocks of Niger and Nigeria. There is a sedimentary hiatus at the base of the Paleogene and the Danian is not preserved (Dikouma et al., 1993). Formation names for Niger and Nigeria from several publications (Kogbe et al., 1976; Reyment, 1980; Reyment and Schöbel, 1983; Adetunji and Kogbe, 1986; Mateer et al., 1992; Moody and Sutcliffe, 1993). Unit ages from Cohen et al. (2013).

region as a whole. Where formation names have already been informally applied to units, we have endeavored to retain these names and to define lectostratotype sections. For the pre-Campanian sedimentary units in northeastern Mali, however, we do not have sufficient new information to define lectostratotype sections or to formalize these units. Thus, we simply provide a brief review of such units and show how they correlate with others in the basin (fig. 3). Facies analysis of Upper Cretaceous–Paleogene units across Mali has been presented in detail previously by our team (Tapanila et al., 2008), and the five repeated facies described for the rocks initially in that paper are again referenced in the sections below. We stress that further fieldwork is required to produce a more in-depth regional correlation among the rocks of Mali, Niger, and Nigeria.

Biostratigraphy has historically been and continues to be the basis for dating these Upper Cretaceous–Paleogene sediments (e.g., Radier, 1959; Krasheninnikov and Trofimov, 1969; Berggren, 1974; Petters, 1977; Reyment, 1979; Boudouresque et al., 1982; Bellion et al., 1990; O'Leary et al., 2006; Claeson et al., 2010) because the field area lacks volcanic sediments for radiometric dating. Thus, ongoing identification of index fossils, taxa that are restricted in time, abundant, and widely distributed geographically (Levin, 2003), has been essential. We denote our fossil discoveries relevant to age determinations with each formation below. Microfossil-based biostratigraphy, including very important contributions on Foraminifera (Krasheninnikov and Trofimov, 1969; Berggren, 1974), Ostracoda (Damotte, 1991; Damotte, 1995), Ostracoda and Foraminifera

TABLE 1

Localities from the 1999 and 2003 expeditions that yielded fossils resulting in publications. Geographic coordinates, age range and fossils identified to date are listed (higher clades provided here, more specific taxonomy within the text or other papers). See plate 1 for lithology by locality except for Mali-6 and -12, which and are older than the Late Cretaceous–Eocene focus of this paper (see Bamford et al., 2002; and O'Leary et al., 2004a). The asterisk (*) indicates a type specimen is part of the fauna. Appendix 3 lists localities examined by us for microfossils.

Locality	Coordinates	Age	Formation(s)	Ichnotaxa & Plantae	Invertebrates	Vertebrata
Mali-1	N 19° 54' E 00° 25'	Campanian-Paleocene	Tichet, Ménaka, Teberemt	*Thalassinoides; Skolithos*	Echinodermata; Ammonitida; Gastropoda, Sorbeoconcha, Latrogastropoda; Bivalvia, Archiheterodonta	
Mali-3	N 19° 37' E 00° 12'	Campanian-Paleocene	Tichet, Ménaka, Teberemt	*Thalassinoides; Skolithos*	Echinodermata; Gastropoda, Sorbeoconcha	
Mali-4	N 19° 37' E 00° 12'	Campanian-Paleocene	Tichet, Ménaka, Teberemt	*Teredolites clavatus;* *Thalassinoides*	Echinodermata	
Mali-5	N 19° 39' W 00° 04	Paleocene	Teberemt			Crocodyliformes, Dyrosauridae (*)
Mali-6	N 18° 40 E 02° 43'	Upper Jurassic-Lower Cretaceous	Continental Intercalaire	Gymnospermae, Podocarpaceae		
Mali-7	N 16° 45' E 02° 30'	Campanian-Paleocene	Tichet, Ménaka, Teberemt		Echinodermata; Nautilida; Ammonitida; Bivalvia, Ostreida, Arcida, Palaeoheterodonta, Archiheterodonta, Cardioidea	Chondrichthyes, Elasmobranchii, Batomorphii; Actinopterygii, Pycnodontiformes; Sarcopterygii, Ceratodontiformes
Mali-8	N 16° 34' E 02° 23'	Campanian-Maastrichtian	Tichet, Ménaka	*Gastrochaenolites ornatus;* vertebrate coprolites; *Linichnus serratus;* *Knethichnus parallelum*	Ammonitida	Chondrichthyes, Batomorphii; Actinopterygii, Pycnodontiformes, Osteoglossiformes, Percomorphi; Sarcopterygii, Ceratodontiformes; Crocodyliformes, Dyrosauridae
Mali-10	N 16° 19 E 02° 46"	Paleocene-Eocene	Teberemt, Tamaguélelt, Continental Terminal		Bivalvia, Ostreida	Actinopterygii, Pycnodontiformes, Osteoglossiformes
Mali-11	N 16° 18' E 02° 45'	Paleocene-Eocene	Teberemt, Tamaguélelt, Continental Terminal		Nautilida; Gastropoda Sorbeoconcha, Cerithioidea; Bivalvia, Ostreida, Pectinida, Myida	Chondrichthyes Batomorphii; Actinopterygii, Pycnodontiformes, Tetraodontiformes, Percomorphi
Mali-12	N 20° 48 E 00° 10"	Upper Jurassic-Lower Cretaceous	Continental Intercalaire			Dinosauria, Titanosauridae; Crocodyliformes

Locality	**Coordinates**	**Age**	**Formation(s)**	**Ichnotaxa & Plantae**	**Invertebrates**	**Vertebrata**
Mali-16	N 16° 48’ E 00° 58’	Paleocene-Eocene	Teberemt, Tamaguélelt, Continental Terminal	vertebrate coprolites	Echinodermata; Nautilida; Bivalvia, Myida and Venerida	
Mali-17	N 16° 48’ E 00° 59’	Paleocene	Teberemt	Angiospermae (Fabaceae)	Echinodermata; Nautiloidea; Gastropoda, Cerithioidea, Latrogastropoda, Neogastropoda, Vetigastropoda; Bivalvia, Ostreida, ?Arcidae, Pectinida, Palaeoheterodonta, Imparidentia, Myida	Chondrichthyes, Batomorphii; Sarcopterygii, Ceratodontiformes; Testudines, Pleurodira, Bothremydidae (*)
Mali-18	N 16° 49’ E 01° 04’	Paleocene	Teberemt	*Thalassinoides; Gastrochaenolites ornatus;* vertebrate coprolites	Echinodermata; Nautilida; Gastropoda, Cerithioidea; Bivalvia, Ostreida	Crocodyliformes; Dyrosauridae
Mali-19	N 16° 50 E 01° 06”	Paleocene	Teberemt	*Thalassinoides; Gastrochaenolites ornatus;* vertebrate coprolites	Echinodermata; Bivalvia, Pectinida, Archiheterodonta	Actinopterygii, Pycnodontiformes; Sarcopterygii, Ceratodontiformes; Squamata, Nigerophiidae (*)
Mali-20	N 17° 34’ E 00° 14 ‘	Paleocene-Eocene	Teberemt, Tamaguélelt, Continental Terminal	*Gastrochaenolites ornatus;* vertebrate coprolites		Actinopterygii, Pycnodontiformes; Halecostomi; Osteoglossiformes; Siluriformes; Aulopiformes; Sarcopterygii, Ceratodontiformes; Squamata, Palaeophiidae, Serpentes indet.; Crocodyliformes, Dyrosauridae; Mammalia, Hyracoidea, “Plesielephantiformes”
Mali-21	N 17° 42 E 00° 20”	Paleocene-Eocene	Teberemt, Tamaguélelt, Continental Terminal		Nautilida; Gastropoda, Vetigastropoda; Bivalvia, Ostreida, Myida	

(Bellion et al., 1989), and fossil pollen (Boudouresque et al., 1982), forms the primary temporal structure for the correlation of these Malian rocks.

An examination of sediments we collected by L. LeVay and L. Edwards did not yield significant biostratigraphically useful microfossils, such as calcareous nannoplankton, dinocysts, or fossil pollen (appendix 3). The only identifiable findings were from rocks of localities Mali-11, which yielded nonspecific palynodebris, and Mali-17 unit 3, which yielded an indeterminate species of the dinocyst *Spiniferites*. The latter ranges from the Cretaceous through the present (Paleobiology Database, 2018) and is simply consistent with other, more refined, age constraints we discuss below. E. Theriot also examined our sediment samples for diatoms and found no informative results. Thus, in the absence of more biostratigraphically informative microfossil discoveries, our biostratigraphic contributions are based exclusively on macrofossils.

CONTINENTAL INTERCALAIRE: Kilian (1931) first used the term Continental Intercalaire to refer to the extensive succession of poorly dated nonmarine deposits exposed across much of West Africa (see also Lefranc and Guiraud, 1990; Mateer et al., 1992). These beds typically lie above Carboniferous marine deposits and below Cenomanian marine strata associated with flooding of the Trans-Saharan Seaway (hence the name, which describes an interleaving or "intercalation" of nonmarine strata between marine beds). Bellion et al. (1989) identified two distinct stratigraphic units that compose the Continental Intercalaire in northern Mali (see fig. 3): the red conglomerate of Tezzoufi (Permian–Middle Jurassic) and an unnamed overlying complex of multicolored clays and limey sandstones (Upper Jurassic–Lower Cretaceous). Those authors also identified a disconformable contact between the top of the Continental Intercalaire and the overlying sequence of Upper Cretaceous marine units. Bellion et al. (1989) placed the contact between these two units at the first appearance of gypsum horizons.

These deposits are, however, poorly exposed in Mali, and limited to the northern portions of the Taoudenit and Iullemmeden basins. Continental Intercalaire rocks were documented in the well log "Ansongo-1" (Elf-Aquitaine, 1979), which bisected the sediments of the central part of the Gao Trench (appendix 2). In this log, the Continental Intercalaire was estimated to be as much as 1500 m thick, and of similar character to the deposits observed elsewhere in outcrop. We described an extensive petrified forest from the upper part of this succession based on our collections at locality Mali-6 (Bamford et al., 2002), as well as new titanosaurian dinosaurs from locality Mali-12 (O'Leary et al., 2004a). Additional details about the sedimentology of this unit are available in those publications. Petters (1977) discussed the equivalents of these beds in Nigeria, synthesizing work by Kogbe et al. (1976), as the Illo and Gundumi formations, noting that the former also contains fossil wood (see also Mateer et al. (1992)). There is currently very poor age control on the Continental Intercalaire rocks in Mali and further refinement of its age is out of the scope of this paper.

UNNAMED UPPER CRETACEOUS CONTINENTAL DEPOSITS: Radier (1959) described a series of Upper Cretaceous continental deposits dominated by ferruginous sandstones and shales, minor bedded gypsum units, thin siliceous limestones with gastropods, and sandy mudstones with large vertebrate bones near the Iullemmeden Basin to the northeast of Ménaka. Similar deposits were also identified by Bellion et al. (1989), and briefly by our team in the northwestern part of the study area in the Taoudenit Basin. These beds were also encountered in several water wells and in the "Ansongo-1" well (Elf-Aquitaine, 1979) where they reach up to 250 m thick. The water well cuttings have been identified as unfossiliferous, and have not been described in detail.

In our examination of outcrops, we did not identify the contact between these beds and the base of the overlying formation (described below), nor was the contact observed in the "Ansongo-1" well report or other water well logs

(Elf-Aquitaine, 1979). However, based on the "Ansongo-1" well report and brief notes made by Radier (1959: 349), we interpret a conformable relationship between these beds and the overlying formation. The term "Continental Hamadian" has been used (e.g., Mateer et al., 1992: fig. 8) to describe these rocks, but the term is so poorly defined that we do not advocate for its continued use and do not apply it here. This formation is poorly dated, with an age constraint derived largely from superposition and broad regional correlation. Further refinement of its age was out of the scope of our work.

TICHET FORMATION: We propose the name Tichet Formation (fig. 4) for the sandstone unit that makes up the base of what has been considered a succession of Campanian-Maastrichtian rocks across Mali (e.g., Moody and Sutcliffe, 1993; figs. 3–5). These deposits were originally described by Monod (1939) and Radier (1959) and later mapped as part of the late Mesozoic "PGi" by Bassot et al. (1981). Bassot et al. (1981) mapped these deposits as a continuous swath along the flanks of the Adrar des Iforas massif across the Taoudenit and Iullemmeden basins through the Gao Trench. The name "Tichet" refers to the well and village located on the northwestern side of the Tilemsi Valley on the far eastern margin of the Taoudenit Basin, which is ~40 km north of the proposed type locality (fig. 1D).

The Tichet Formation is defined herein as the sequence of buff to locally green and pale orange-colored, cross-bedded sandstones typified by large-scale inclined foresets located between the upper Cenomanian gypsiferous deposits and the base of the overlying Ménaka Formation (defined below). The basal contact of the Tichet Formation has not been directly observed anywhere in the field area but is placed above the highest-bedded gypsum unit of putative Cenomanian-Senonian age (sensu Bellion et al., 1989). The bedded gypsum unit crops out above the Continental Intercalaire. The upper contact of the Tichet Formation is defined herein as the top of the uppermost sandstone bed (or siltstone locally) below the thinly bedded succession of paper shales and carbonates of the Ménaka Formation. The contact is sharp and distinctive in outcrop, where it is commonly characterized by an intensely bioturbated, deeply oxidized contact.

Type locality and stratotype section. The type section is located at the base of the large escarpment ~40 km north of Tichet and another reference section was measured at a locality that we termed Mali-1 (fig. 2; plate 1), located at 19° 28.918′N / 0° 19.499′E. The lower contact of the Tichet Formation cannot be observed in the type area and has not been observed directly anywhere by the authors. Three reference sections for the Tichet Formation have been measured and described: from a nearby locality in the Tilemsi Valley at Mali-3/4; and at two localities in the Iullemmeden Basin (Mali-7 and -8) to the west of Ménaka, all of which expose the top of the formation (fig. 2; plate 1).

Description of the sedimentology. The Tichet Formation is characterized by fine-grained, cross-bedded sandstones and siltstones of facies 1 and 2 of Tapanila et al. (2008). In three out of the four areas where the Tichet Formation was studied (Mali-3/4, -7, -8) the basal portion of the formation is dominated by a succession 5–15 m thick of distinctive, large-scale (~5–7 m), gently dipping (5°–8°) sandstone beds (Facies 1). These beds dip to the south at Mali-3/4, and to the northeast at Mali-7 and Mali-8. Laterally, the large-scale inclined sandstone beds transition along strike, as well as stratigraphically upward into horizontally stratified sandstone beds with trough cross-stratification and herringbone cross-stratification (also Facies 1). The facies has abundant impressions of the ichnofossil *Teredolites* (fig. 5), a type of fossilized boring formed in wood. *Skolithos* burrows are also present in this unit and most abundant toward the base of the gently inclined sandstones (fig. 4D). Complex root traces become more common toward the top of the unit, along with indistinct burrows. In the type locality, the horizontally bedded sandstones of Facies 1 are conformably overlain by a 20–25 m thick, upward-coarsening succession of shales (Facies

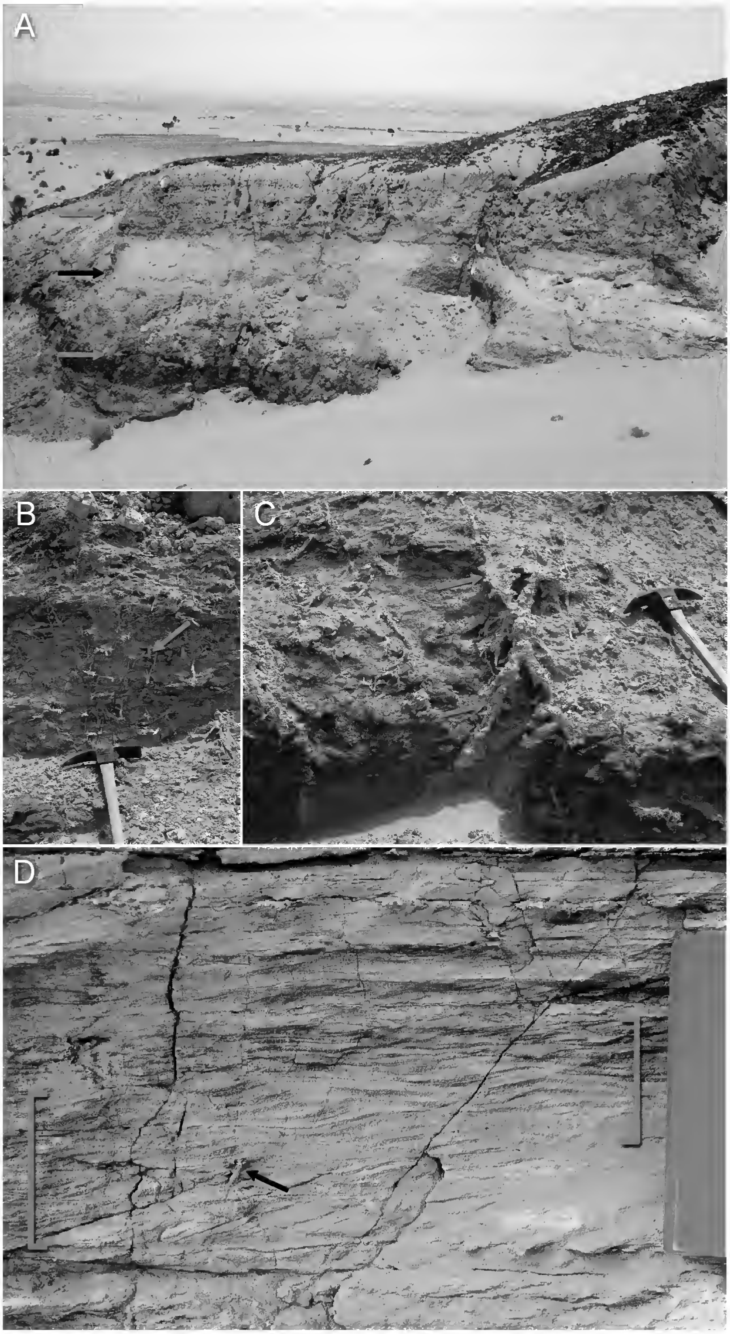


FIGURE 4. Basal deposits of the Upper Cretaceous–Campanian Tichet Formation near the base of the Mali-1 and Mali-3/4 sections in the Tilemsi Valley, Taoudenit Basin: **A,** 5 m thick alternating succession of rhizoturbated sandstones (yellow arrows) and unmodified, horizontally laminated and ripple cross-laminated sandstones (black arrow) interpreted as estuarine to tidal flats with evidence of mangrove roots; **B–C,** close-up photos of intensely rhizoturbated sandstone beds from A showing fossil mangrove root networks (red arrows) among indeterminate invertebrate burrows; **D,** horizontally laminated to ripple cross-laminated sandstone with climbing ripples (red brackets) and the ichnofossil *Skolithos* sp. (black arrow) represented by an isolated vertical burrow.

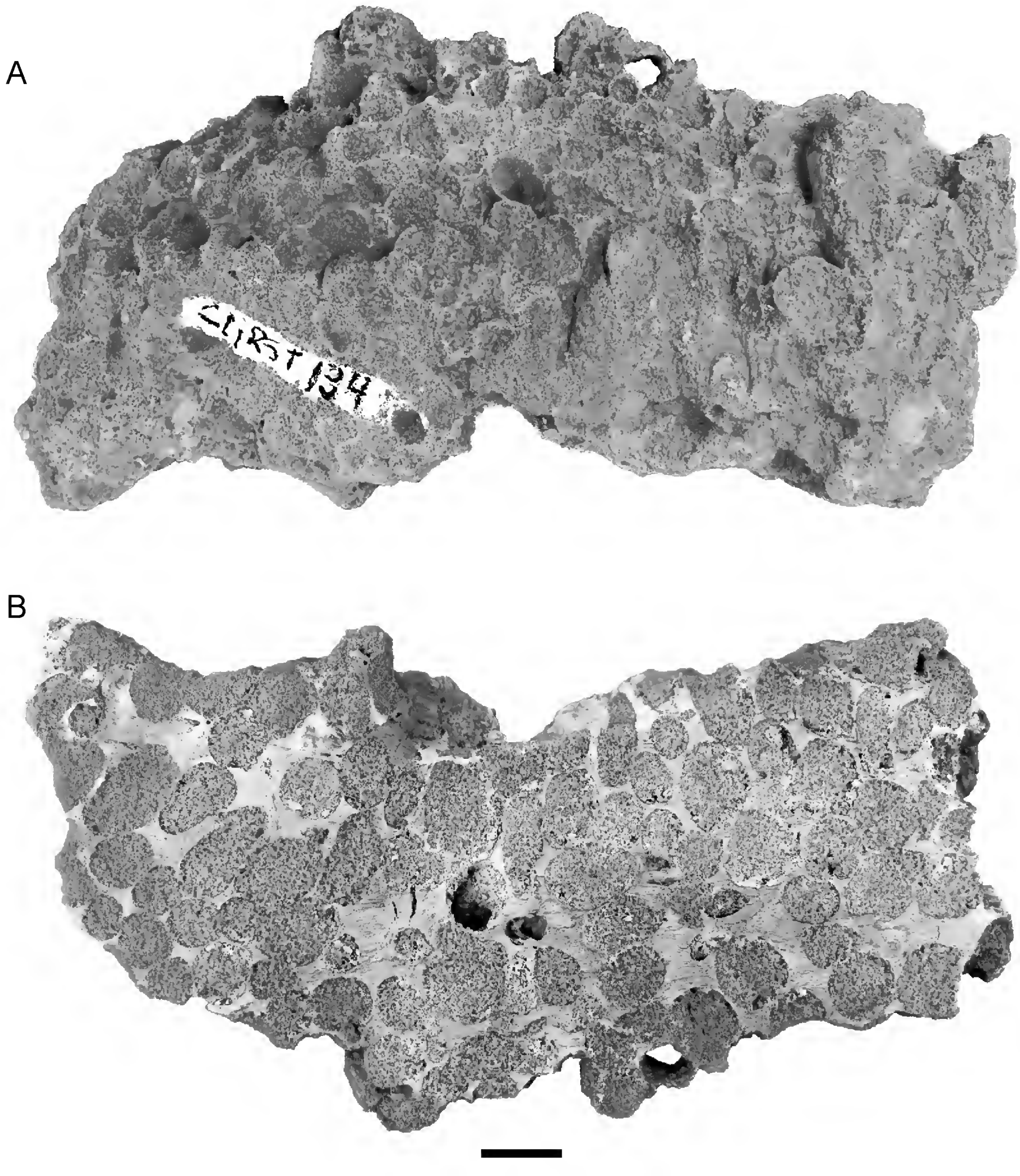


FIGURE 5. Example of intensely bored fossil wood fragment from the Upper Cretaceous–Campanian Tichet Formation collected at locality Mali-4; the clavate (sock-shaped) borings are *Teredolites clavatus* (CNRST-SUNY 134). **A,** external view of wood with borings mostly filled in with medium-grained sand, and **B,** internal view of bored wood after sectioning. Scale bar = 1 cm.

2), followed by siltstones and sandstones of Facies 1. These units are also pervasively bioturbated with evidence of oxidized burrow and root networks. Bedding is commonly lenticular, with alternating mudstone and siltstone couplets. These uppermost facies are not observed in the Iullemmeden Basin sections, where the total thickness of the formation is less than half that observed in the Taoudenit Basin section, the latter reaching a maximum exposed thickness of 30 m. The Tichet Formation is completely absent from the Gao Trench. In all studied sections, the top of the formation is characterized by a deeply oxidized, heavily bioturbated capping sandstone/siltstone, which sits sharply beneath the first paper shale or thin limestone bed of the Ménaka Formation.

Interpretation of the sedimentology. The base of the Tichet Formation is interpreted to represent a deltaic system, with the large-scale, gently inclined sandstone beds indicative of delta front depocenters. Laterally and stratigraphically overlying these deposits are the horizontally bedded sandstones with trough cross-stratification and herringbone cross-stratification, as well as overlying mudstone and siltstones with tidal couplets and complex root networks, which we interpret as lower delta plain deposits. The lenticular bedding and paired sand-silt couplets are interpreted as low-energy tidal deposits consistent with a lower delta plain setting; and the complex, oxidized, root networks are interpreted as mangrove root systems similar to those reported from Paleogene deposits from the Fayum region in Egypt (Bown and Kraus, 1988). We interpret this series to represent a single continuous delta system of freshwater that drained into the Trans-Saharan Seaway because there is a north to south along-strike facies change from lower delta plain deposits at Mali-1 to delta front deposits at localities Mali-3/4.

The point source for the drainage was to the north, most likely out of the Adrar des Iforas massif. Interestingly, a similar pattern is observed at localities Mali-7 and -8, where the basal, gently inclined sandstones are interpreted as delta front deposits and the overlying horizontally bedded sandstones and siltstones are interpreted to be south-southwest directed, prograding upper delta plain deposits. We also interpret the more western localities of Mali-7 and -8 to have been connected to the same delta system, but as laterally correlative delta lobes connecting to a large, bird-mouth type delta system that was most likely sourced from a second river system draining out of the Adrar des Iforas Mountains to the south. We can not, however, rule out that the Tichet Formation deposits observed at all four localities could be part of a single, progradational delta system. The distinctive oxidized, intensely bioturbated top of the formation, which is sharply overlain by paper shales or thin limestone beds, was interpreted by Tapanila et al. (2008) as a sequence boundary and superimposed marine flooding (transgressive) surface.

Discussion of the sedimentology. Petters (1977) observed that the Taloka Sandstone, the Nigerian equivalent of the Tichet Formation, also contained *Skolithos* trace fossils and worm burrows as well as *Thalassinoides*, bivalves, and vertebrate fossils. Petters (1979: 755) interpreted the Taloka Formation as "coastal plain–beach–shallow sublittoral" environment. Mateer et al. (1992: fig. 8), in an overview paper, interpreted the Continental Hamadian, a poorly defined group of continental sediments (see also Greigert, 1966), as extending through the Campanian in Mali and contacting a Taloka Formation at the start of the Maastrichtian. We do not follow that terminology here because of the insufficient precision associated with the term "Continental Hamadian."

Age based on biostratigraphy. The oldest rocks in our composite section, and the only ones that we interpret as Cretaceous, are found in both the Taoudenit and Iullemmeden basins. To date, we have identified no index fossils and no vertebrate or invertebrate macrofossils in the Campanian-Maastrichtian rocks of the older Tichet Formation. The fossilized burrows, both crustacean and otherwise, and root casts have yet to provide temporal information. Our correlation of the continuity of Tichet Formation beds suggests that it is one of the formations in our study area that is time transgressive. Its age assessment is based on a combination of constraints placed by fossils from units above and our sequence stratigraphic correlation (i.e., the sandstones vary in time and are represented at the margins of the basin during sea-level regression), and on comparisons with published sequences from Nigeria and Niger (Kogbe, 1991; Moody and Sutcliffe, 1991; 1993). Lithostratigraphy indicates that this formation lies between the highest gypsiferous facies of the Continental Intercalaire (upper Cenomanian) and the lowest paper shales of the Maastrichtian Ménaka Formation. Comparisons with published ages on correlative sequences from Nigeria and Niger suggest a Campanian-Maastrichtian age for these rocks in Mali.

Ménaka Formation: The name "In-Fargas Formation" was originally used by Moody and Sutcliffe (1991) to describe the Upper Cretaceous succession across Mali, however, those authors later referred to this set of rocks as the "Cheit Keini Formation" (Moody and Sutcliffe, 1993). Although Moody and Sutcliffe (1993: figs. 3, 5) suggested that they intended to restrict the Cheit Keini Formation to the uppermost Maastrichtian, it was not in the end further specified in their paper and it remained unclear whether Moody and Sutcliffe (1991, 1993) were referring to all Upper Cretaceous strata in Mali or whether they were specifically referring to only the uppermost Cretaceous deposits. They only provided an idealized graphic log for these deposits across the combined Mali and Sokoto (Nigeria) regions, which suggested that they may have been referring only to the uppermost deposits (because it does not match what we have observed in Mali). However, no detailed type section was included. The details on the idealized graphic log for this unit could not be matched to the observed stratigraphy anywhere in the study area our team examined. The graphic log is also difficult to reconcile with measured stratigraphic sections and descriptions for the uppermost Cretaceous strata provided by Radier (1959) and Bellion et al. (1989). Moody and Sutcliffe (1993) described the Cheit Keini Formation as mostly sandstones of shallow marine and deltaic influence, which is more consistent with what is observed lower in the Upper Cretaceous stratigraphy (what we have described above as the Tichet Formation). Adding to the confusion, the Tichet Formation, or indeed any deposit fitting a similar description, does not crop out near In Fargas, closest to this study's localities Mali-18 and -10.

Thus, to avoid confusion and perhaps error, we suggest that the terms In Fargas Formation and Cheit Keini Formation are to be avoided and propose that both terms be abandoned as they have not been formally defined and do not match the observed stratigraphy. Hence, we propose the name Ménaka Formation for the uppermost Cretaceous deposits in northern Mali (figs. 2, 6; plate 1). These deposits were originally described by Radier (1953) and mapped as the "PGi" by Bassot et al. (1981), who demonstrated their continuous distribution across the Taoudenit and Iullemmeden basins through the Gao Trench along the flanks of the Adrar des Iforas massif. The name "Ménaka" refers to the large village to the southeast of the Adrar des Iforas mountains, on the far western margin of the Iullemmeden Basin, to the south of localities Mali-7 and Mali-8 (figs. 1D, 2). The Ménaka Formation is defined herein as the sequence of shales and marly limestones, with minor sandstones and phosphate conglomerates, that overlies the Tichet Formation and is overlain by the Teberemt Formation (see below; fig. 6). The basal contact of the Ménaka Formation area typically overlies the large-scale delta foresets of the Tichet Formation, but locally sits above the highest sandstone unit of the Tichet Formation. The top contact of the Ménaka Formation is easily recognized across most of the study area, as it is placed below a silicified limestone bed with distinctive karstic weathering that is regionally traceable. This bed was termed the "Terrecht I" limestone bed by Radier (1959), who also used it as a marker horizon. Using Foraminifera and Ostracoda in the Tichet region of Mali, Bellion et al. (1989), con-

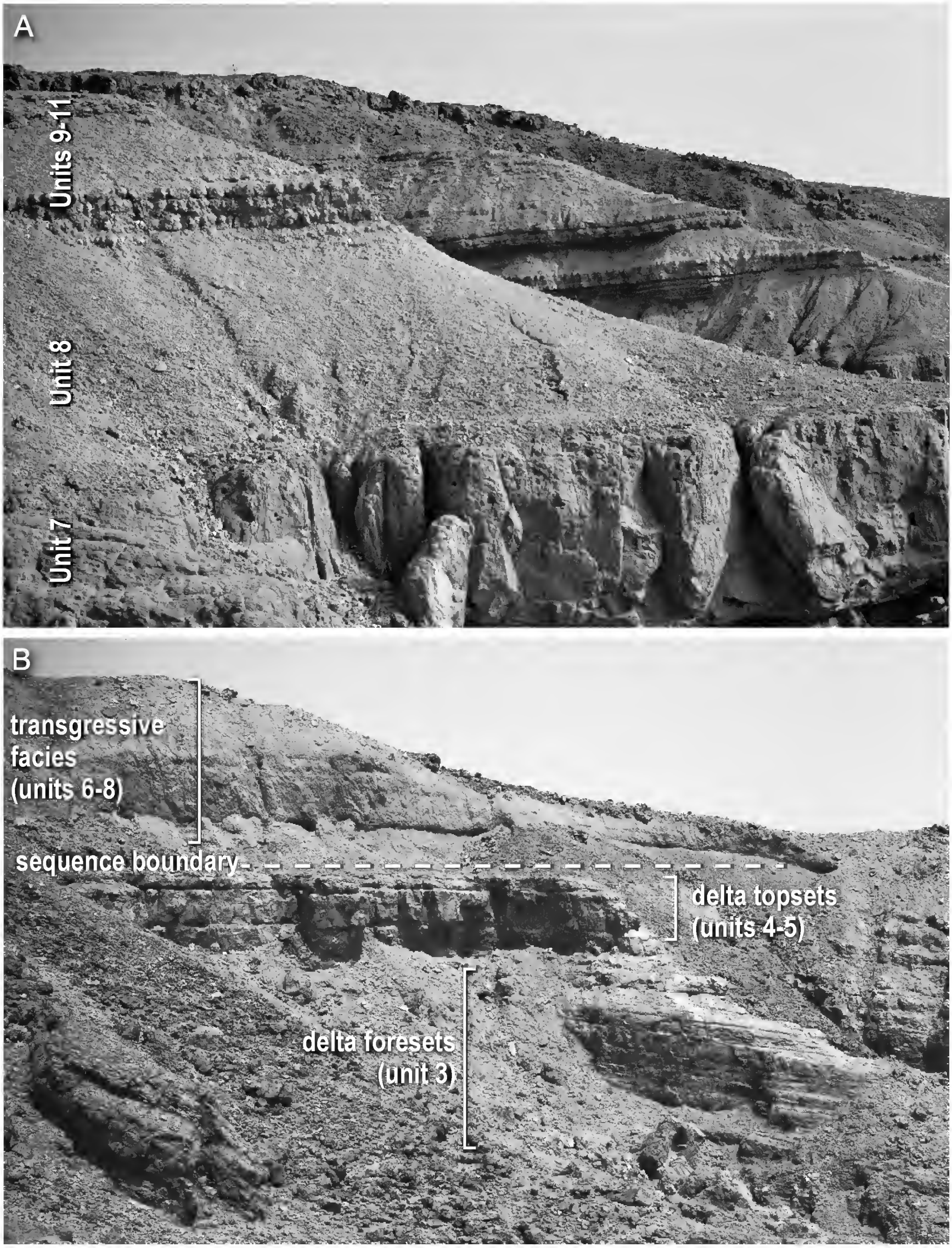


FIGURE 6. Outcrops in the northern Iullemmeden Basin illustrating the sedimentology through the middle part of the Maastrichtian Ménaka Formation, locality Mali-7. The 40 m thick succession has yielded ammonite and shark specimens that are critical for biostratigraphy. **A,** upper part of section with thick bioturbated siltstones (unit 7), and richly fossiliferous, thin, blocky marls and interbedded shale units (units 8–11); **B,** lower part of the section showing: pronounced, dipping delta foresets, overlain by horizontally bedded delta topsets, then capped by a sequence boundary, and followed by overlying transgressive, deeper water shales and marls.

sistent with Radier (1959), placed the K-Pg boundary at the top of what we are now calling the Ménaka Formation, specifically, at the top of the karstic "Terrecht I" limestone.

In the field we observed a weakly karstic to silicified capping limestone bed that we consider to be the "Terrecht I" bed. We have marked the top of "Terrecht I" as the approximate location of the K-Pg boundary in our correlated section (plate 1) following Bellion et al. (1989). The karstic nature of the bed suggests a prior subaerial exposure possibly due to sea-level fall, a characteristic consistent with an unconformity. We have no further data to confirm or refine this hypothesis for the position of this boundary other than the biostratigraphy we discuss below.

Type locality and stratotype section. The type section is located at the base of the large escarpment ~25 km north of Ménaka at the locality know as Mali-7, which is located at 16° 44.837′N/2° 31.471′E. The lower contact of the Ménaka Formation lies directly above a deeply oxidized, highly bioturbated, horizontally bedded sandstone at the top of the Tichet Formation, and extends to the top of a distinct orange paper shale unit just below the base of the Teberemt Formation. Three reference sections (plate 1) for the Ménaka Formation have been measured and described, including a nearby section (locality Mali-8) a few kilometers to the south of type locality, and two more in the Tilemsi Valley (localities Mali-1 and -3/4).

Description of the sedimentology. The Ménaka Formation is characterized by a heterogeneous succession of paper shales, thin, interbedded shales and marly limestones, thicker limestones, and siltstones and fine sandstones, corresponding respectively to facies 1–4 of Tapanila et al. (2008). The entire formation tends to be recessive in outcrop, particularly the paper shales, with the thin marly limestones and thicker limestones forming benches. Limestones become more abundant and thicker upsection. The paper shales are extremely fissile and preserve abundant mollusk shells (fig. 7), foraminifera, ostracods, shark and other fish teeth, and ray dental plates. The most unusual unit is a thin phosphate conglomerate (fig. 8) with abundant vertebrate bones and coprolites (for further detail see Hill et al., 2008; Claeson et al., 2010). The interbedded shales and marly limestones (mollusk and echinoid packstones; Facies 3 of Tapanila et al., 2008) are often pale yellow in color and highly fossiliferous, although moldic preservation is quite common. Some beds preserve extensive carpets of aligned high-spire turritellid gastropods, which were commonly observed to have their long axes oriented in a subparallel N-S orientation (fig. 9). Large oysters, some forming small reefs, are common, as are more isolated bivalves, echinoderms, and ammonites. Distinctive *Thalassinoides* burrow networks are common in these facies (examples of this trace fossil from the Teberemt Formation are figured below), along with a range of other indistinct burrows. Significantly, although there are phosphatic marls and shales in the Ménaka Formation, the phosphate conglomerate is the only one observed anywhere in the study area below the K-Pg boundary. A single, well-preserved ammonite was found in place from a thick limestone unit (locality Mali-8) above this bed (Claeson et al., 2010). This limestone has a karstic weathering pattern suggesting subaerial exposure. The Ménaka Formation is nearly twice as thick in the Iullemmeden Basin as it is

FIGURE 7. Example of a nautiloid steinkern from a limestone unit (locality Mali-8 unit 12, Facies 3) at the top of the Maastrichtian Ménaka Formation.

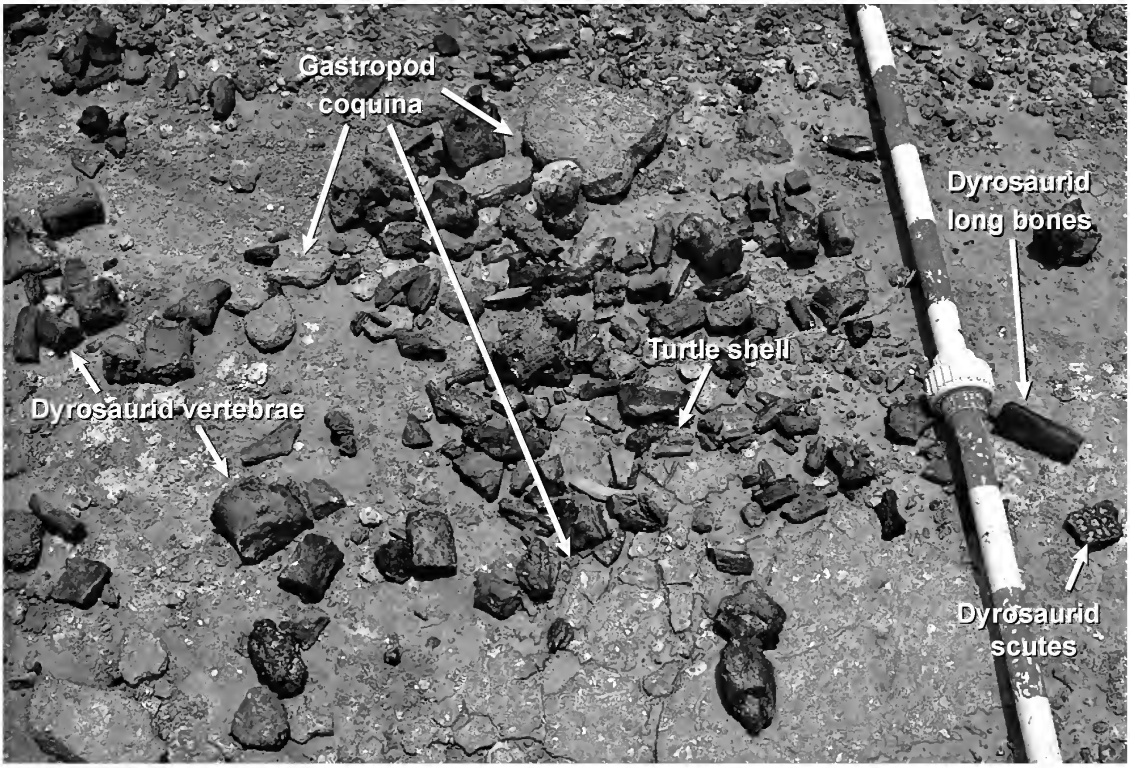


FIGURE 8. Fossiliferous phosphate conglomerate bed of the Maastrichtian Ménaka Formation, locality Mali-8, showing a typical assemblage of dyrosaurid crocodyliform and turtle fossils. The fossiliferous phosphate conglomerate rests directly on a well-lithified gastropod coquina (see also CT scan, fig. 9). This is the only such phosphate bed we have identified in the Mesozoic part of our section; others are present in the Paleogene.

in the Tilemsi Valley. In the Tilemsi Valley, the section appears to be a bit more condensed (i.e., characterized by slower depositional rates), but there is more limestone and less shale. This formation was not observed in the Gao Trench area. A pale yellow sandy limestone at locality Mali-5, which produced an exquisitely preserved dyrosaurid skull, may be part of the Ménaka Formation. However, this locality displayed little vertical relief making it difficult to correlate laterally with the rest of our section. Because the locality is geographically mapped among the "Pgi" sediments of Bassot et al. (1981), we currently consider it to be age-bracketed as Maastrichtian-Paleocene in age.

Interpretation of the sedimentology. We interpret the Ménaka Formation as representing shallow, normal-to-restricted marine deposits of the Trans-Saharan Seaway, which formed during the T5 cyclothem (the latter is discussed below). We consider most facies to have been formed in a sublittoral environment, with the fossiliferous limestone beds interpreted to have been rapidly buried due to storm reworking, while the phosphate conglomerate bed likely formed due to storm reworking and stratigraphic condensation (Tapanila et al., 2008). We interpret the base of the formation to have been deposited during a period of rapid marine transgression. The phosphate conglomerate bed just noted as concentrated by storm reworking, represents a condensed section, and is associated with a maximum-flooding surface. The upper part of the formation is interpreted to represent a highstand systems tract (fig. 6). We see a distinctive pattern of deepening upward, indicating a sea-level rise and deepening seawaters because we find deltaic facies (of the underlying Tichet Formation) overlain by more offshore muds. As noted above, the gastropod assemblage captures fossil shells oriented in a formation that is subparallel and opposed. Our interpretation of this finding is that waves in water, which flowed roughly perpendicular to the long axis of the shells, created transport alignment of the shells. Our paleocurrent measurements on the shells indicate that at locality Mali-8, waves were moving in N-S or S-N orientation. These types of gastropods are often, although not exclusively, indicators of nearshore, shallow water environments, such as the upper intertidal zone. The presence of in situ oysters also supports this suggestion.

This formation ranges from over 20 m of strata dating from what may be the latest Campanian–early Maastrichtian in the Iullemmeden Basin, to only 10 m of deposits restricted to the late Maastrichtian in the Taoudenit Basin. We interpreted the time-transgressive nature of these deposits based on facies stacking patterns described above. The Gao Trench contains no surface-exposed Ménaka Formation rocks based on our mapping to date.

Discussion of the regional correlations. Moody and Sutcliffe (1993: table 1) summarized different naming schemes for Upper Cretaceous rocks in the Sokoto Basin, Nigeria, and noted that the "*Mosasaurus* shales" of Niger are the equivalent of the Dukamaje Formation of Nigeria. The Dukamaje Formation of Kogbe et al. (1976: 248) is ascribed to the Rima Group, which we consider a lateral equivalent of the Ménaka Formation, and to have been deposited in swampy waters that were brackish, with occasional interruptions of fully marine water. Petters (1977) described the laterally equivalent Dukamaje Formation of Nigeria as representing two distinct environments: a hypersaline lagoon or estuary and a system of ponds. Petters (1977: 756) also mentioned that the Wurno Formation, also a Ménaka Formation equivalent in Nigeria, showed signs of greater marine influence and might also contain the K-Pg boundary, however, he noted that there was insufficient evidence for this conclusion. Mateer et al. (1992) made important inroads correlating Cretaceous terrestrial rocks in West Africa. They used two sets of terminologies: Terme 1–3 (from Radier, 1959; see also Moody and Sutcliffe, 1993), as well as Taloka, Dukamaje, and Cheit Keini (which we replace herein with the Ménaka Formation) formations from oldest to youngest for what we consider to be Ménaka Formation rocks. We have not recovered mosasaurs in our field area.

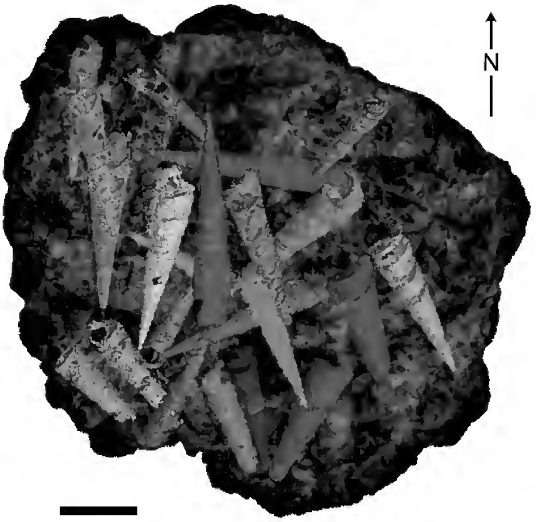


FIGURE 9. CT scan-based reconstruction of fossil shells of Gastropoda, Turritellidae (CNRST-SUNY 114), Turritellinae indet. "C" in a limestone from the Maastrichtian locality, Mali-7 unit 12, of the Ménaka Formation. Specimens present in lithified beds as extensive carpets of aligned high-spire forms that appear to have been rapidly buried, oriented with their long axes in a subparallel north-south orientation. Technical details on the scan are in text. Scale bar = 1 cm and the rock specimen is 2 cm deep (into page).

Age based on biostratigraphy. As discussed by Bellion et al. (1989) the presence of the ammonite *Libycoceras crossense* in the uppermost beds of what we now call the Ménaka Formation supports the assignment of a Maastrichtian age. Integrating information on foraminiferans from the Tilemsi Valley with these ammonite discoveries, Bellion et al. (1989) and Damotte (1991) noted specifically that the limestone layer called "Terrecht I" by Radier (1953, 1959) is in the Maastrichtian. Additionally, the presence of the elasmobranch *Schizorhiza stromeri*, which we recovered low in the section, is further indication of a Maastrichtian age for the Ménaka Formation.

Ménaka Formation sediments in the Iullemmeden Basin have yielded particularly numerous index fossils. As noted, the oldest index fossils come from paper shales of Facies 2 at the base of the Ménaka Formation at locality Mali-7 unit 10, and represent sawfish shark teeth identified as *Schizorhiza stromeri* (Claeson et al., 2015). This shark species occurs widely in, and is restricted to, Maastrichtian deposits in Africa, Iraq, and North and South America (Cappetta, 1987; Wueringer et al., 2009; Claeson et al., 2010). Below the occurrence of *Schizorhiza stromeri* (see locality Mali-7 in plate 1) we tentatively propose that the beds may extend into the Campanian following Moody and Sutcliffe (1991) and lithostratigraphic correlations with Nigeria (Petters, 1979; Moody and Sutcliffe, 1993).

At the same locality that yielded *Schizorhiza stromeri*, in the overlying succession of interbedded marls and shales (Unit 11, which represents Facies 4), we collected samples of the index fossil mollusk, *Trigonarca* sp. The genus *Trigonarca* is known only from the Cretaceous (Newell, 1969). Slightly higher upsection from a chalky marl at the top of unit 11 at locality Mali-7, we also collected the regular echinoid, *Echinotiara perebaskinei*. Lambert and Perebaskine (1930) previously reported this taxon from the Gao region, and more recently Smith and Jeffery (2000) described it as distributed throughout Africa and the Arabian Peninsula during the Maastrichtian only.

The next-youngest index fossil, the ammonite *Libycoceras*, comes from Ménaka Formation rocks in both the Taoudenit Basin, locality Mali-1, again, from a paper shale of Facies 2 near the top of the section, and from the Iullemmeden Basin localities Mali-7 and -8. The specimen, which was collected in situ at Mali-8, from a massive limestone (Facies 3, unit 12), is the only one with sutures well preserved enough to make a species-level identification as *Libycoceras crossense*. This specimen is illustrated in Claeson et al. (2010: fig. 2 [the taxonomic name in that paper was misspelled]). The genus *Libycoceras* ranges from the Campanian through the Maastrichtian, and the species *Libycoceras crossense* ranges from the late Campanian through middle–?late Maastrichtian (Zaborski and Morris, 1999). Finally, the Ménaka Formation in the Iullemmeden Basin section also yielded a tooth from the vertebrate Maastrichtian index fossil, *Cretalamna* (*Serratolamna*) *maroccana*, a lamniform shark (Case and Cappetta, 1997; Shimada, 2007; Claeson et al., 2010) that we collected from shale beds (Facies 3) very high in the section (Mali-7 unit 14). *Cretalamna* is found in both Maastrichtian and Danian rocks, but is much rarer from Maastrichtian ones (Belben et al., 2017). Its presence in the section at Mali-7 suggests the rocks are Maastrichtian in age or possibly younger. In previous publications (e.g., Hill et al., 2008), we identified "*Turritella* sp." as an index fossil of the Ménaka Formation, however, based on our taxonomic revisions here we now recognize these specimens only as Turritellidae indet. with several genera likely represented (see Systematic Paleontology). The presence of Turritellidae, a clade that appeared in the Cretaceous and remains extant today (Allmon, 2011), provides only the broadest biostratigraphic indicator that the Ménaka Formation is at most Cretaceous in age. Although the local section at Mali-3/4 in the Taoudenit Basin has 30 m of Ménaka Formation rocks, it yielded neither index fossils nor other invertebrate or vertebrate macrofossils.

TEBEREMT FORMATION: The name Teberemt Formation was suggested by Moody and Sutcliffe (1991) for the heterogeneous succession of open marine shales and carbonates that comprises the Paleocene across Mali (fig. 10). These deposits were originally described by Radier (1953) and mapped as part of the "PGs" Paleo-

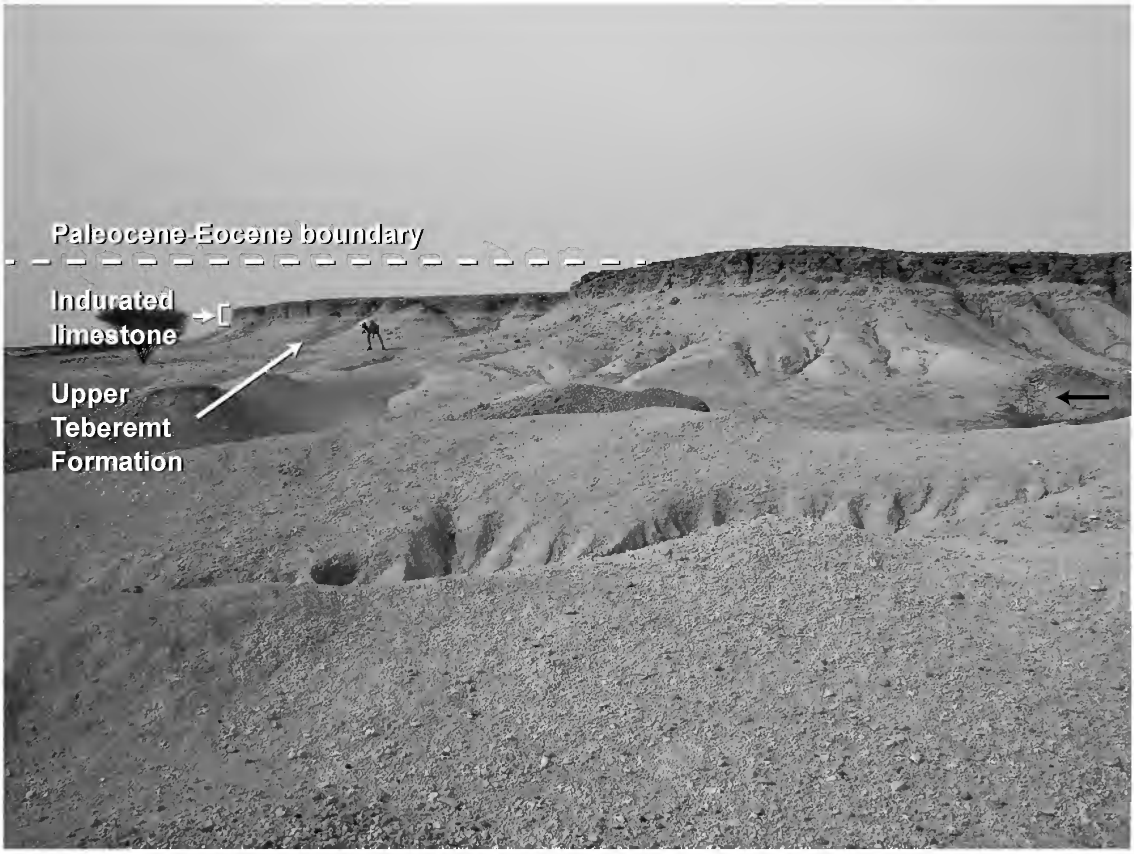


FIGURE 10. Paleocene Teberemt Formation near Samit at the Mali-17 locality, which contains numerous vertebrate fossils. Exposure of the upper part of the Teberemt Formation (~10 m thick) capped by indurated limestone (also known as "Terrecht II"; here formally considered part of the Teberemt Formation) that lies just below the Paleocene-Eocene boundary. Black arrow indicates approximate stratigraphic location of turtle fossil shown in figure 11. Person in image denotes scale.

gene by Bassot et al. (1981) as a continuous swath across the Taoudenit and Iullemmeden basins, through the Gao Trench, along the flanks of the Adrar des Iforas massif. Moody and Sutcliffe (1993) provided a composite graphic log for Mali and northern Nigeria showing the basic stratigraphy of the Teberemt Formation, but neither the rationale for the name "Teberemt" nor a type locality was provided in either of their publications (Moody and Sutcliffe, 1991, 1993). The stratigraphy they described is generally consistent with what we observed for this interval; however, Moody and Sutcliffe (1991, 1993) did not adequately demonstrate the range of lithofacies and the lithological complexity associated with this unit. Rather than establish a new name for this stratigraphic unit, we have opted to designate and describe a lectostratotype section and retain the existing name. The Teberemt Formation is defined herein as the ~12–17 m thick heterogeneous succession of carbonates, shales, and phosphates that overlie the top of the Ménaka Formation and sit below the overlying Tamaguélelt Formation (defined below). The basal contact of the Teberemt Formation is defined by an extensive 1–5 m thick limestone bed that lies disconformably atop the Ménaka Formation. The upper contact of the formation is distinguished by a similar 1–5 m thick limestone bed.

Type locality and lectostratotype section. We have documented a complete lectostratotype section through the Teberemt Formation at Mali-18 in the Gao Trench, which we herein designate as the type area. In addition, we have identified and measured a second reference section in the Gao Trench at locality Mali-19, along with two partial reference sections in the Iullemmeden Basin at Mali-7 and Mali-10, and one additional reference section in the Taoudenit Basin at Mali-3/4. The lectostratotype section at Mali-18 can be observed at N 16°49′36.0″, E 1°04′14.9″.

Description of the sedimentology. The Teberemt Formation is observed across the entire study area, characterized by a high level of facies change in and between sections. The base of the formation is easily identified by the karstic, weathering limestone bed referred to as the "Terrecht I" bed by Radier (1959). This bed preserves abundant echinoids and oysters. As noted above, an exquisitely preserved dyrosaurid crocodyliform skull found at Mali-5 (Brochu et al., 2002) may be from this bed but is now of uncertain placement in the section and is possibly from the Maastrichtian Ménaka Formation. Above this bed, the section is dominated by interbedded shales, carbonates, and phosphate conglomerates, with the latter facies limited to the Gao Trench area. The Teberemt Formation forms a series of recessive slopes made up of shales and distinctive benches, which are capped by limestones. An incredibly abundant fauna has been recovered from this formation, including numerous vertebrates, such as fish, crocodyliforms, and snakes from the phosphate conglomerates and an abundant invertebrate fauna from the shales and carbonates, dominated by echinoids, oysters, nautiloids, gastropods, and foraminiferans (Gaffney et al., 2007; Hill et al., 2008; McCartney et al., 2018). Interesting taphonomic situations are preserved, including turtle skeletons encrusted with ostreidan bivalves (fig. 11). Fossil wood is also present and trace fossils abound, particularly well-developed *Thalassinoides* burrow networks. At the top of the section, and included in the Teberemt Formation, is a distinctive karstic limestone bed, which Radier (1959) referred to as the Terrecht II bed. This bed forms a capping bench across much of the region.

Interpretation of the sedimentology. The Teberemt Formation represents shallow, normal to restricted marine deposition within the Trans-Saharan Seaway. Deposition possibly transpired during the sea level change of the T6 Cyclothem (discussed below). The cyclic nature of the deposits and repeating nature of the phosphate conglomerate beds in this interval was interpreted by Tapanila et al. (2008: see also Sequence Stratigraphy section below) to represent portions of three retrogradational parasequences. As with the Ménaka Formation, the phosphate conglomerate beds are considered to have formed as storm-reworked condensed sections associated with periods of maximum transgression of the seaway.

Discussion of the sedimentology. A depositional hiatus has been suggested by the lack of Danian taxa found in Nigeria and elsewhere at the base of the Teberemt Formation (Bellion et al., 1989; Damotte, 1991). Petters (1977: 756) described the Dange, Kalambaina, and Gamba formations of Nigeria (sometimes called the "Sokoto Group"), which we interpret as the lateral equivalents of the Ménaka Formation, as indicative of a marine transgressive environment. Regarding the Dange Formation in particular, Petters (1977) interpreted it as estuarine, citing as evidence a faunal mixture of marine and freshwater fishes. He interpreted the Kalambaina rocks as indicating a warm, more open, shallow sea, and that the Gamba Formation represented a return to more estuarine conditions.

Age based on biostratigraphy. As noted above, our own microfossil analysis yielded the dinocyst *Spiniferites* indicating that the Teberemt Formation is at most Cretaceous. The exact transition between the Ménaka Formation and the younger Teberemt Formation is imprecise in our field area and likely represents an unconformity. Four of our local sections, Mali-1 and Mali-3/4 in the Iullemmeden Basin, and Mali-7 and Mali-8 in the Taoudenit Basin, nonetheless, extend through

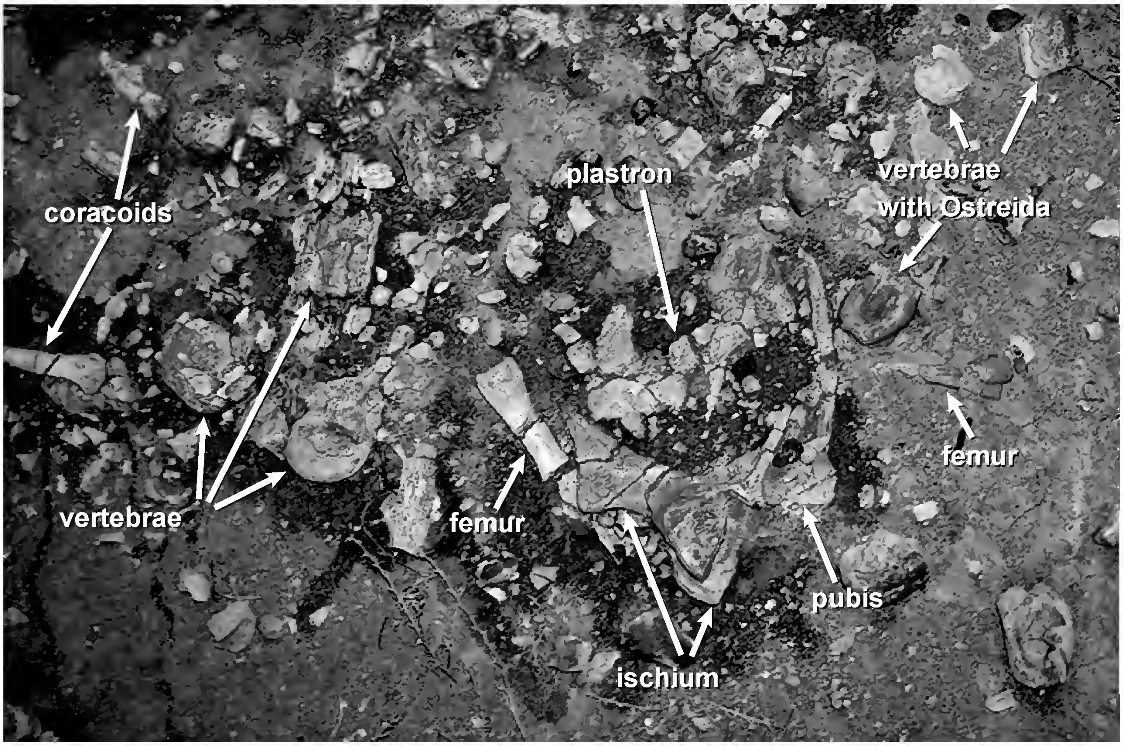


FIGURE 11. Fossilized bothremydid turtle skeleton, disarticulated, but in situ, from the Paleocene Teberemt Formation at the Mali-17 locality near Samit, Mali. Note encrustation of vertebrae and other bones by ostreidan bivalves. Color and contrast of bones has been enhanced.

this boundary and contain rocks of both the Ménaka Formation and the overlying Teberemt Formation.

Perhaps the most complex issue pertaining to the Teberemt Formation geology is the placement of the K-Pg boundary and assessment of the hypothesis that Danian rocks are absent in this section. Bellion et al. (1989) reported, based on work in the Malian region of Tichet, that their stratigraphically lowest Paleocene microfossil samples yielded two species of the planktonic foraminiferan *Globorotalia*, indicating the beds were Paleocene and specifically Montian ("Zone P2"). These Montian units are stratigraphically superposed on the "Terrecht I" limestone (discussed above as Maastrichtian) below and extend all the way to a capping "Terrecht II" limestone (Radier, 1953; 1959). Bellion et al. (1989; see also Damotte, 1991) concluded that Danian deposits are missing and that there is a regional gap in sedimentation in the earliest Paleocene (also referred to as a "Lower Paleocene gap" [Dikouma et al., 1993: 105]), as evidenced in part by desiccation cracks at the top of Terrecht I, which, as noted above, we corroborated. The bed called "Terrecht II" by Radier (1953, 1959), which is part of the Teberemt Formation, has been dated as Paleocene by the benthic foraminiferan *Ranikothalia bermudezi* (Bellion et al., 1989, 1990; Damotte, 1991; also discussed in O'Leary et al., 2006).

The Teberemt Formation rocks, including those at the base of the sections in the Gao Trench, contain index fossils in their lowest beds. The limestone beds (Facies 3) at the base of the Teberemt Formation in all three field areas contain specimens of the echinoid *Oriolampas michelini*. In their review, Smith and Jeffery (2000) documented *O. michelini* from Paleocene (typically Thanetian) deposits throughout West Africa (i.e., Nigeria, Niger, Sudan, Algeria, and Mali) and from the French Pyrenees. At Mali-7 this echinoid species is found approximately 10 m higher than the specimen of *Cretalamna maroccana* noted above. *Oriolampas michelini* also persists in younger beds, again in limestones (Facies 3), in the Teberemt Formation. The Gao Trench contains the most diverse set of index fossils for the Teberemt Formation. Two nautiloids contribute biostratigraphic information: *Cimomia reymenti* from Mali-17 shales (Unit 3, Facies 2) and *Cimomia ogbei* from younger Mali-18 limestones (Unit 8, Facies 3). These species have Maastrichtian and Paleocene ranges (Adegoke, 1977). *Linthia sudanensis*, which is found in limestones of both the Gao Trench (at Mali-16, -17, -18 and -19) and the Iullemmeden Basin (at Mali-7), has been attributed an early-late Paleocene age with a questionable Maastrichtian occurrence (Smith and Jeffery, 2000). Although in our prior work (e.g., Hill et al., 2008) we identified specimens of the mollusk *Ostrea multicostata* from limestones (Facies 3) of several Gao Trench localities (Mali-16, -17, and -18), in our revised identifications here we find that these specimens are actually of more ambiguous taxonomic attribution (i.e., no more specific than Ostreidae) and do not contribute to the biostratigraphy we propose.

Our observations and research are consistent with the inference of an unconformity, if only due to the negative evidence that we have recovered no macrofossils that are clear biostratigraphic indicators of the Danian. We were not, however, able to collect mollusks in a sufficiently systematic way to perform a thorough search for a faunal signature indicative of the Danian. One such pattern was reported by Hansen (1988: 40), albeit in relatively offshore environments, who observed that "Early Paleocene faunas have a much higher percentage of species in the Carditidae, Ostreidae and Turritellidae than is seen in the Late Cretaceous and the remainder of the Paleocene." Nor are our mollusk species identifications refined enough to compare with species-level studies of Danian mollusks at other latitudes such as that of Cope et al. (2005) in rocks of southern Illinois or that of Río and Martínez (2015) in Patagonia, Argentina.

Likewise, for echinoids, Smith and Jeffery (1998) reported that a number of echinoid clades made their last appearance in the Danian before extinction. Danian occurrences of echinoids are generally rare from North Africa. However, the foraminiferan-dated Danian Upper Tar Member of the Zimam Formation in the Hamadah Basin of Libya preserves echinoids *Hemiaster nucleus*, *H. frontacutus*, and *Echinobrissus pannonicus* in shallow marine, carbonate ramp facies (Megerisi and Mamgain, 1980; Hallett and Clark-Lowes, 2016). In Egypt, Danian shales and marls that compose the upper Dakhla Formation (previously called the Blätterthone Formation) preserve the echinoids ?*Coelopleurus fourtaui*, ?*Micraster* sp., *Hemiaster chargensis*, and *Cidaris* (Tantawy et al., 2001; Quaas, 1902). We can report that none of these genera, let alone species, are found in the Malian sections despite generally good preservation and abundance of echinoids collected during our expeditions. Finally, no mammal fossils have been recovered from Paleocene rocks of Mali, and no other vertebrate fossils currently serve as indices for the Paleocene in Malian sediments.

TAMAGUÉLELT FORMATION: Radier (1959) originally referred to the deposits overlying the Paleocene carbonates (Teberemt Formation) as the "Schistes Papyreuses"; however, Moody and Sutcliffe (1991) expanded on the description of these deposits to include the phosphates and siltstones that accompany the paper shales in many places, calling this succession the Tamaguélelt Formation. The origin of the name "Tamaguélelt" was not provided, nor was a type locality designated. Moody and Sutcliffe (1993) provided a composite graphic log for Mali and northern Nigeria showing the basic stratigraphy of the Tamaguélelt Formation. The stratigraphy those authors described is generally consistent with what has been observed by us for this interval; however, their work does not adequately demonstrate the range of lithofacies and the lithological complexity associated with this unit. Rather than establish a new name for this stratigraphic unit, we have opted to designate and describe a lectostratotype section. The Tamaguélelt Formation is defined herein as the ~12–17 m thick heterogeneous succession of carbonates, shales, and phosphates that lies above the top of the Teberemt Formation and below the overlying Continental Terminal (fig. 12). The basal contact of the Tamaguélelt Formation is easily recognized as it sits just above the karstic, weathered "Terrecht II" limestone unit. The upper contact of the formation is distinguished by ferruginized sandstones at the base of what are informally called the Continental Terminal sediments.

Type locality and lectostratotype section. We have documented a complete lectostratotype section through the Tamaguélelt Formation at Mali-20 in the Tilemsi Valley (Taoudenit Basin), which we herein designate as the type area. In addition, we have identified and measured a second reference section in the Gao Trench at Mali-16. The lectostratotype section at Mali-20 can be observed at N 17°35′35.3″, E 0°14′59.7″.

Description of the sedimentology. The Tamaguélelt Formation is dominated by a succession of paper shales and siltstones, punctuated by several phosphate conglomerates of widely varying thickness, as well as by rare sandstone beds (fig. 12). The paper shales are mostly unfossiliferous, although Radier (1959) did report a bivalve from these beds. The paper shales also have a much more orange to yellow color than those of the Ménaka or Teberemt formations, and often contain iron oxide nodules. Bioturbation in the formation is largely limited to the thin siltstone beds, which are abundantly bioturbated. The top of the formation is characteristically black in color with heavy iron- and manganese-oxide concretion development. The lowest phosphate conglomerate in the formation is the thickest and most richly fossiliferous unit in the study area, preserving a remarkable abundance of isolated vertebrate bones, including rare mammal fossils. This bed was described in detail in several papers by our team (Tapanila et al., 2004; O'Leary et al., 2006; Tapanila et al., 2008; McCartney et al., 2018).

Interpretation and discussion of the sedimentology. The Tamaguélelt Formation appears to rest conformably on the Teberemt Formation based on our observations, and we placed the contact at the top of the regionally distinctive limestone marker horizon known as the "Terrecht II" bed. We interpret the Tamaguélelt Formation as having been deposited in a shallow, and slowly filling, marine to possibly brackish embayment of the Trans-Saharan Seaway during the early to middle Eocene, and to lie conformably over the Teberemt Formation. Tapanila et al. (2008) interpreted this unit to represent the final pulse of the Trans-Saharan Seaway in Mali during the highstand-systems tract of the T6 cyclothem (discussed below). The phosphate beds present in this formation, which are geographically widespread and remain to be mapped in full, may be among the most extensive macrofossil bone beds known on Earth based on our comparisons with other deposits (Tapanila et al., 2008). The presence of mammals that may have had an amphibious but not fully marine lifestyle (O'Leary et al., 2006; Sanders et al., 2010) attests to the nearshore nature of these deposits, while the range of taxa present in the phosphate conglomerates encompasses marine to possibly brackish water settings.

Age based on biostratigraphy. The phosphate deposits of the Tamaguélelt Formation do not preserve calcareous shells (discussed more below in the section "Fossiliferous Phosphate Facies"), and invertebrates from other layers have not been informative for biostratigraphy. The Tamaguélelt Formation has been somewhat tenuously dated as Eocene based on vertebrate fossils. We consider the phosphate conglomerates 3 m above "Terrecht II" limestones the oldest Eocene beds in our section (Tapanila et al., 2008).

We do not repeat here the extensive discussion by Patterson and Longbottom (1989) of the challenges of dating this formation using biostratigraphy. Those authors reached the conclusion that the formation is either Ypresian or Lutetian in age. In Longbottom's (1984: 23) review of Malian pycnodonts she cautioned that

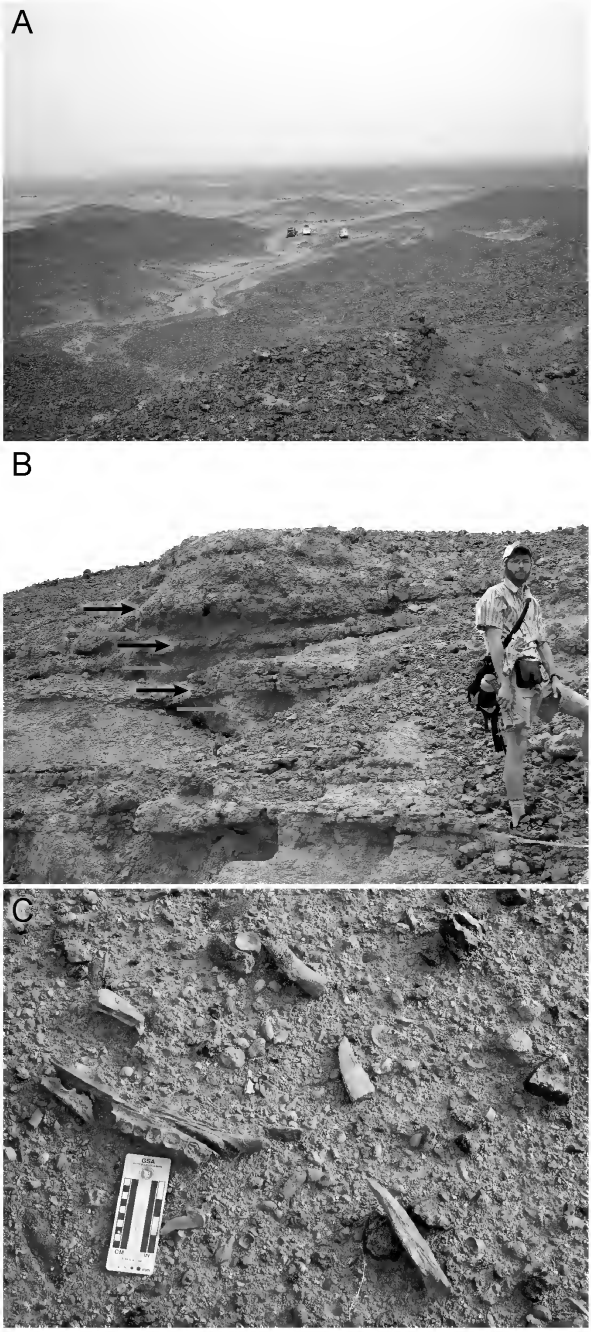


FIGURE 12. Type section of the Tamaguélelt Formation at locality Mali-20, southeastern edge of Tilemsi Valley, near the transition between the Taoudenit Basin and the Gao Trench. **A,** view from the top of the formation to the field camp down the largely recessive, shale-dominated succession (vehicles indicate scale); **B,** multiple layers of phosphatic shales and phosphate conglomerates (black arrows) interbedded with marls and shale (yellow arrows); and **C,** deflation surface at the top of a phosphate conglomerate revealing rich assemblage of disarticulated phosphatic pebbles, vertebrate bones and coprolites.

the clade is "not useful for dating purposes." Longbottom (1984: 23) also wrote that *Pycnodus bowerbanki*, and two other pycnodont species she identified in Mali– *P. variabilis* and *P. munieri*, "are known elsewhere from the Landenian to the Lutetian," suggesting the faunal signature was consistent with an early Eocene age for the phosphates, but one that brought no great precision to the age of these beds. This pycnodont-based evidence for a Ypresian age for the Tilemsi Valley Tamaguélelt sediments was repeated by Moody and Sutcliffe (1993).

Although mammals from this formation are certainly too fragmentary to serve as index fossils, we note here that Sanders et al. (2010) assigned the proboscidean fossils from Mali (more discussion on this below) to "Plesielephantiformes" incertae sedis and noted that the Malian fossils resemble phosphatheres and daouitheres, both of which are early Eocene clades. O'Leary et al. (2006) reported that the lowest bone-producing bed in this formation is only 3 m above the Paleocene "Terrecht II" limestone layer (described above in the Teberemt Formation) and concluded that the combination of sediment thickness and vertebrate fossils found continue to suggest an early Eocene age.

POST-EOCENE "CONTINENTAL TERMINAL" DEPOSITS: We did not collect thoroughly in sediments that were younger than Eocene, as our reconnaissance in such rocks yielded only a few invertebrate fossils. The informal term "Continental Terminal" was proposed by Kilian (1931) and reviewed by Lang et al. (1990) who emphasized that this detrital unit of Cenozoic rocks is often poorly dated. The deposits consist of ferruginous oolitic sandstones, oxidized siltstones, and dark red mudstones that span the Eocene to Pliocene and contain few fossils (Kilian, 1931; Lang et al., 1990). We have observed that these deposits are significantly altered by laterite pedogenesis, obfuscating original sedimentary structures and lithology, and resulting in probable leaching of biominerals (carbonate) from fossil shells.

SYNTHESIS OF SEDIMENTOLOGY AND SEQUENCE STRATIGRAPHY

Trans-Saharan Seaway sediments were deposited as part of a carbonate platform with rocks that precipitated in situ, as well as significant siliciclastic sediments that eroded from adjacent uplifted rocks. Sedimentary sequences across the entire area the sea covered are sands, clays, shales, and limestones characterized by broad similarities in regional stratigraphy and sedimentology (see Radier, 1959; Greigert, 1966; Petters, 1977; 1979). Our close inspection has revealed that, nonetheless, significant sedimentological variations in thickness, lateral and vertical facies stacking patterns, and depositional environments exist across the Taoudenit Basin, the Gao Trench, and the Iullemmeden Basin, and that these had not been characterized in detail prior to our work (e.g., O'Leary et al., 2006; Hill et al., 2008; Tapanila et al., 2008).

Fundamental to our correlation among these three geographic regions has been detailed facies analysis (Tapanila et al., 2008) revealing the presence of five repeated facies and strata that occur in fining-upward sequences (table 2; figs. 13, 14) tracking transgressive-regressive cycles of the Trans-Saharan Seaway (Moody and Sutcliffe, 1993). In our model, as seas retreated after a transgression, exposed land was then eroded. The coastal plain expanded and contracted during four to six cyclothems, leaving sequences of marine and nonmarine sediments. We have interpreted these sequences as representing a variety of ancient nearshore continental, marginal marine, and open marine environments (Tapanila et al., 2008), interpretations that have informed our paleobiological interpretations of fossils collected (Tapanila et al., 2004; Gaffney et al., 2007; Hill et al., 2008; Tapanila et al., 2008). These interpretations are consistent with the hypothesis that the Trans-Saharan Seaway was likely never deeper than 50 m (Krasheninnikov and Trofimov, 1969; Berggren, 1974; Tintant et al., 2001).

TABLE 2

Facies observed in Late Cretaceous-Eocene sediments of northern Mali and an interpretation of the ancient nearshore marine environments they represented (see Tapanila et al., 2008).

Facies	Lithology	Environmental interpretation
Facies 1	sandstone and siltstone	tidally influenced shoreline and deltaic environments
Facies 2	paper shale	shallow, normal-to-restricted marine lagoons and open platform settings
Facies 3	mollusk and echinoderm packstone; limestone	oysters in patch reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity
Facies 4	interbedded marl and shale; mudstone and wackestone	shallow, sublittoral open marine settings with water depths <50 m
Facies 5	phosphate conglomerate	shallow marine-to-brackish water phosphorites associated with periods of amalgamation and concentration by storm activity during periods of marine transgression

To discuss our model in detail we use the Iullemmeden Basin section at locality Mali-8 (plate 1) and an idealized version of facies change (fig. 14). The Mali-8 locality consists of approximately 35 m of section deposited along the Trans-Saharan Seaway as part of at least one complete sea-level cycle (T5 Cyclothem of Greigert, 1966), as we have discussed (Tapanila et al., 2008). The base of the section is defined by Facies 1 and its large, inclined, fine-grained sandstone beds with glauconite and petrified wood of delta-front origin (fig. 4). The next 20 m represents deposits of the T5 transgressive systems tract, dominated by thinly laminated shales and marls of facies 2 and 3, which are overlain by phosphatic limestones and the distinctive phosphate conglomerate (Facies 5) representing the maximum flooding surface (condensed section) of the T5 cyclothem. Above that level are open marine, quiet water mudstones and wackestones (Facies 4), suggesting that ammonites found in them are in situ. These beds are followed by storm-generated mollusk and echinoderm packstones (Facies 3) associated with the overlying T5 highstand-systems tract (Tapanila et al., 2008: fig. 3).

This section documents a repeated fining/deepening-upward sequence overlain by extensive bone/coprolite phosphate conglomerates. Phosphate conglomerates at the base of fining-upward sequences represent syndepositional phosphogenesis tied to marine transgression. We suggest that these represent maximum flooding surfaces, and their presence has been important for defining sea-level cyclicity and reconstructing paleogeography. We have established the genetic nature of these surfaces, i.e., that the surfaces formed due to storm concentration in an epeiric setting rather than by the model of upwelling at a continental margin. They could therefore be used, in conjunction with detailed sedimentological investigation of other surfaces and facies, to understand the nature, frequency, and timing of Paleogene sea-level cyclicity (3rd–5th order) in the Trans-Saharan Seaway in Mali (further discussion on this in the GPlates section below). Finally, identifying genetic surfaces has facilitated the correlation of thin, repeated strata across our field area.

Fossiliferous Phosphate Facies

Many of the vertebrate fossil specimens we have described from sites throughout our study area (e.g., at localities Mali-8, -16, -18, -19, and -20) come from Facies 5, the bone, coprolite, and pebble phosphatic conglomerate that ranges in

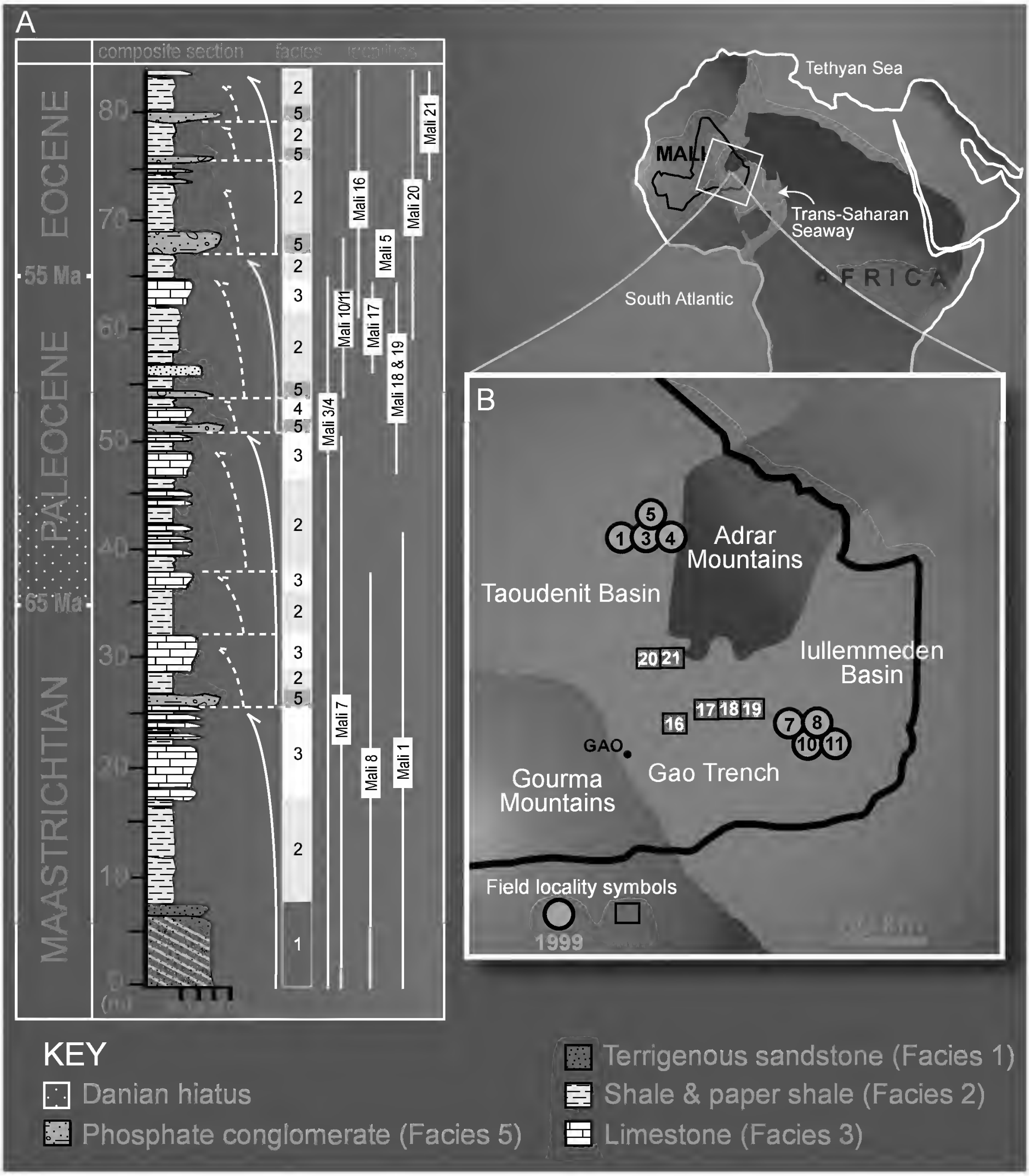
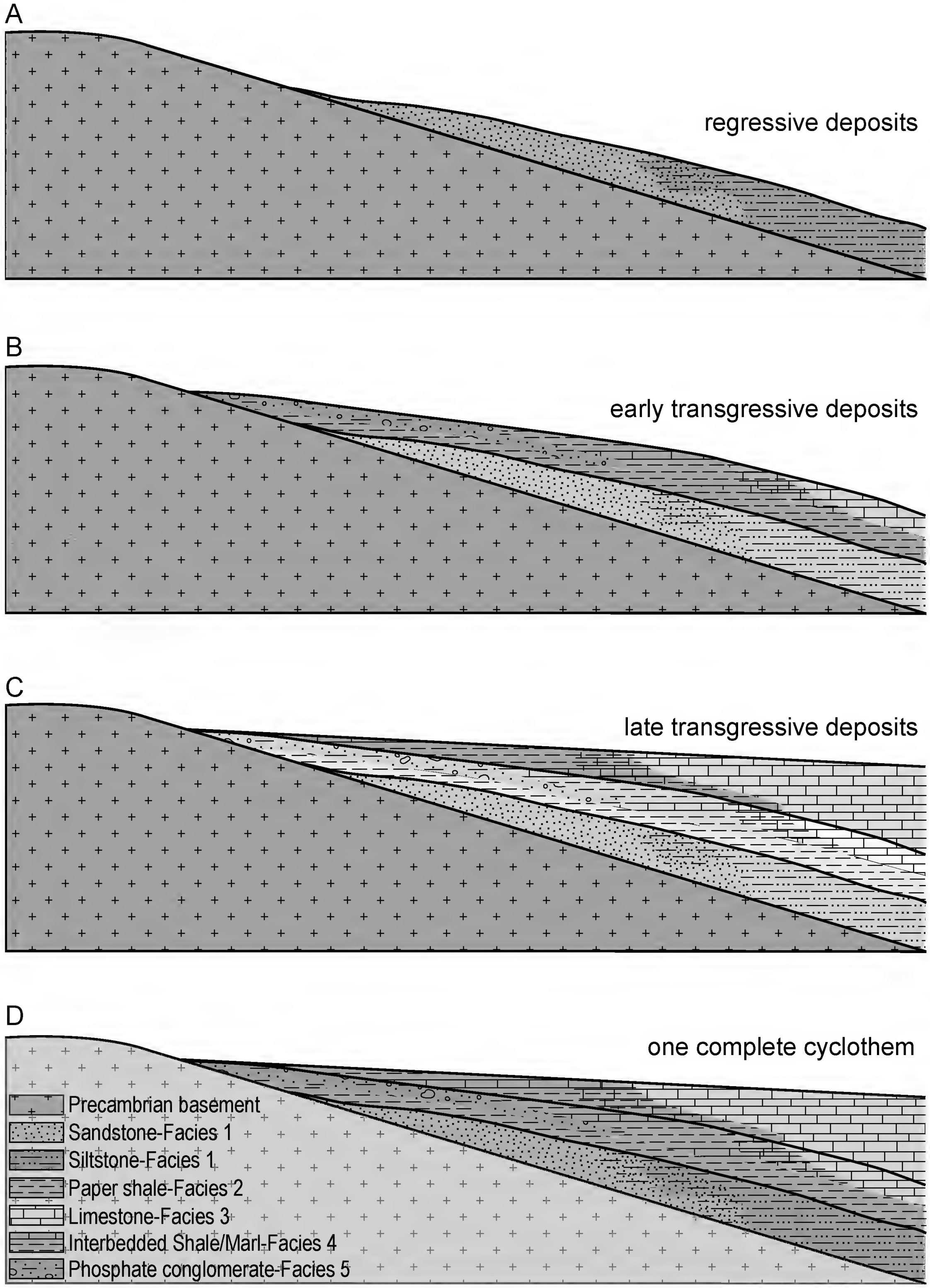


FIGURE 13. The Trans-Saharan Seaway in Mali, interpreted using sequence stratigraphy and our generalized facies model. **A,** repeating facies changes in our composite section and the time span (vertical lines) of particular localities in Mali; and **B,** geographic distribution of those localities in northwestern Mali. Sandstone and phosphate deposits probably formed at different times. During regressions (low sea level), sandstones were deposited on the coast, and during transgressions (rising sea level) at maximum sea level, phosphate conglomerates formed subaqueously in shallow marine areas. Horizontal dashed lines indicate the tops of cyclothems (sequence boundaries), dashed arrows indicate shallowing upward parasequences, and solid arrows indicate sets of parasequences. Dots indicate likely nondeposition during the Early Paleocene (Danian).


A
regressive deposits
B
early transgressive deposits
C
late transgressive deposits
D
one complete cyclothem
Precambrian basement
Sandstone-Facies 1
Siltstone-Facies 1
Paper shale-Facies 2
Limestone-Facies 3
Interbedded Shale/Marl-Facies 4
Phosphate conglomerate-Facies 5

age from the Maastrichtian through Eocene (O'Leary et al., 2006; Hill et al., 2008; Claeson et al., 2010; Hill et al., 2015). This previously unclassified variety of phosphate conglomerate (P_2O_5 content >18%) has been the most intensively studied by us (Tapanila et al., 2008), due to its important bearing on sedimentological and paleontological questions. These strata are separate, decimeter-scale conglomerates that may extend laterally for kilometers and are most common in the post-Cretaceous section (plate 1). They are clast supported and range from unconsolidated to weakly cemented (plate 1; see also fig. 12). Clasts are predominantly granule to cobble sized, but also include pieces of vertebrate bone as large as 25 cm. Bioclast shape and size analysis demonstrated a sorting in the thickest phosphatic deposit: Mali-20 unit 2 (also called "Mali-20a" [Tapanila et al., 2008; McCartney et al., 2018]).

It is noteworthy that coprolites, bones, and bored phosphatic limestone cobbles are the most common constituents of the conglomerate, but that calcareous shelled invertebrates are almost completely absent as body fossils. In one locality studied in detail (again, Mali-20), clasts over 1 cm varied as follows: 27% bone, 20% identifiable coprolite, and 53% indeterminate phosphatic clasts that are likely weathered coprolites (Tapanila et al., 2008). The vertebrate bone consists entirely of disassociated anatomical elements from a range of fossil species that were likely marine to nearshore marine (in order of frequency of occurrence): siluriform catfish, amiids (*Maliamia*), rays, pycnodonts, lungfish, and osteoglossiforms (*Brychaetus*). Mali-20 is also the locality that has yielded rare paenungulate mammal fossils (O'Leary et al., 2006).

Teeth, except myliobatid ray and pycnodont tooth plates and a rare isolated mammal tooth, are also almost completely absent from this deposit, a phenomenon that we have attributed to chemical dissolution during phosphogenesis (Tapanila et al., 2008). Indirect lines of evidence, however, do point to the presence of tooth-bearing vertebrates (e.g., dyrosaurids, amiids) and calcareous invertebrates in the ancient ecosystem. Evidence of toothed vertebrates exists through the presence of numerous jaws with empty tooth sockets (shown below; see also O'Leary et al., 2006; Tapanila et al., 2008). Likewise, evidence of calcareous-shelled invertebrates exists through numerous occurrences of the ichnofossil *Gastrochaenolites ornatus* (see below), a boring into lithoclasts, coprolites, and vertebrate bone, some of which even preserve the external mold of pholadid bivalves (Tapanila et al., 2008).

We have developed a model describing how this peculiar deposit formed. Typically, phosphates form under select circumstances requiring a high threshold concentration of phosphate minerals in shallow marine sediments. The source of the phosphate is generally bone or feces, particularly from carnivorous vertebrates, or plankton with phosphatic tests. These elements are subject to decay, and high concentrations of bone, feces, and plankton tests are required to generate bed-

FIGURE 14. Our carbonate platform model for the Trans-Saharan Seaway in Mali showing one complete and idealized cyclothem through time and the cumulative deposits. Nearshore siliciclastic rocks weathered from the Adrar des Iforas massif at the proximal (shoreward) part of the basin and fine-grained carbonate rocks accumulated in situ primarily from calcareous microorganisms. **A,** regressive deposits formed during late highstand phase as coastline prograded basinward in large delta complexes, depositing thick siliciclastic strata. A sequence boundary associated with sea level fall marks the top of this systems tract; deposits of lowstand systems tracts are conspicuously absent from the basin. **B,** early transgressive deposits; sea level rises faster than siliciclastic sediment is produced, coastline moves furthest inland and fine-grained shales, thin carbonates and phosphate deposits accumulate. **C,** late transgressive deposits; sea-level rise at maximum, shutting off siliciclastic sediments to basin; carbonate production is high, and thick limestone and marl deposits accumulate basinward. In restricted portions of basin, thick phosphate conglomerates form (not shown). **D,** one complete cyclothem. We do not observe rocks representing environments such as reefs, sand distal from shore or very deep ocean sediments and hypothesize that these were absent in much of the study area. Illustration vertically exaggerated to show facies relations and surfaces.

ded phosphates over any appreciable stratigraphic scale. Tapanila et al. (2008) hypothesized that the particular Malian conglomerate formed in a depositional environment with shallow marine to brackish water that lay between fair weather and storm-weather wave base. We interpreted our discovery of a pholadid bivalve, a taxon that requires water of normal marine salinity, as paleobiological evidence that this type of water must have characterized the ancient environment (Tapanila et al., 2004). We presented evidence that the conglomerate represents a long-lived sedimentary deposit that formed under unusual chemical circumstances allowing phosphate-enriched materials (e.g., bone and coprolites containing bone fragments) to be preferentially mineralized on the seafloor. Once lithified, the fossil clasts were concentrated by wave action to form a gravel substrate on the seafloor that was colonized occasionally by rock-boring clams. The assemblage of fossils and coprolites in these deposits, therefore, represents a concentrated (i.e., time-averaged) temporal sample of marine life. For the deposition of these phosphate beds to occur at our localities in Mali, we hypothesized that several variables needed to align (Tapanila et al., 2008):

(1) Bony remains of animals and feces must be prevented from decay on the sea floor, a situation that requires low oxygen conditions to kill or block aerobic bacteria from destroying bones and feces;

(2) Once the low oxygen environment is in place, certain anaerobic or extremophile bacteria feed on the material and convert original bioapatite into mineral apatite (e.g., francolite), thus turning the bones and feces into fossils. This transition occurs on the seafloor relatively quickly in geologic time (Föllmi et al., 1991);

(3) To get thick deposits of phosphate concentrations (i.e., phosphate beds), this deposited material must become concentrated. We hypothesized in Tapanila et al. (2008) that these deposits form at maximum flooding (maximum transgression or high stand). With sea level at its highest there is the greatest accommodation available immediately along the coastline. Sediments from the land sources that could dilute the concentration of phosphates are restricted to the shorelines at the peak of transgression. Importantly, this situation leads to sediment starvation in the more offshore portions of the shallow seaway, meaning that for a brief period, the shallow offshore region is not accumulating siliciclastic detritus, only biological detritus. This sedimentological model creates the scenario needed to generate low oxygen or anoxic conditions. The coalescence of extensive amounts of decaying organic matter containing phosphate feeds a population explosion of aerobic bacteria. However, aerobic bacterial growth becomes self-limiting and the bacteria consume all the resources, ultimately starving their own population;

(4) Finally, as the Trans-Saharan Seaway was also particularly shallow at maximum transgression because it was reaching deeply into the continent interior, for a short period of time, approximately 10 ky, storm events easily impacted and churned up the bottom waters of this seaway (Pufahl et al., 2003). These storms winnow the silt and clay by tossing such minerals back into the water column where they can be redeposited elsewhere (typically further out into the basin where energy is lower). Such events thereby concentrated the larger phosphatized bioclasts, leaving the coprolites and fragmented vertebrate bones to form the conglomerate that we have collected.

Other Noteworthy Fossiliferous Facies

In addition to the phosphate conglomerates, which have produced the greatest volume and diversity of fossil vertebrates from the Trans-Saharan Seaway region of Mali, a number of other facies have been productive for fossil exploration (plate 1; figs. 13, 14). In the Upper Cretaceous-Paleogene sections of all three study regions in Mali, the limestones and shales of facies 4 and 2, respectively, have produced numerous vertebrate and invertebrate fossils. In contrast to the phosphatic facies, the limestones and shales yield the best-preserved specimens, such as numerous intact vertebrate skulls and associated body fossils. Species preserved from Facies 4 include a range of marine vertebrates, from isolated shark teeth to nearly complete dyrosaurid crocodyliform skulls (Brochu et al., 2002) and multiple associated to completely articulated turtles (Gaffney et al., 2001; Gaffney et al., 2007). Moreover, these units have also yielded diverse and well-preserved invertebrate assemblages across the basins, dominated by echinoderms, nautiloids, ammonites, gastropods, bivalves, and oyster beds.

Notes on Taphonomy and Specimen Collection

Specimen Collection. The expeditionary work was restricted to short stays (2–3 days) at each outcrop due to security and proximity to support services. Major priorities were the removal of significant vertebrate fossils and the immediate documentation of the stratigraphic context, including the collection of samples relevant to biostratigraphy. For the collection of vertebrate fossils, we prioritized rare, unusual, and complete specimens. Specimens were almost exclusively surface collected and in some cases were retrieved still entombed in substantial amounts of rock matrix.

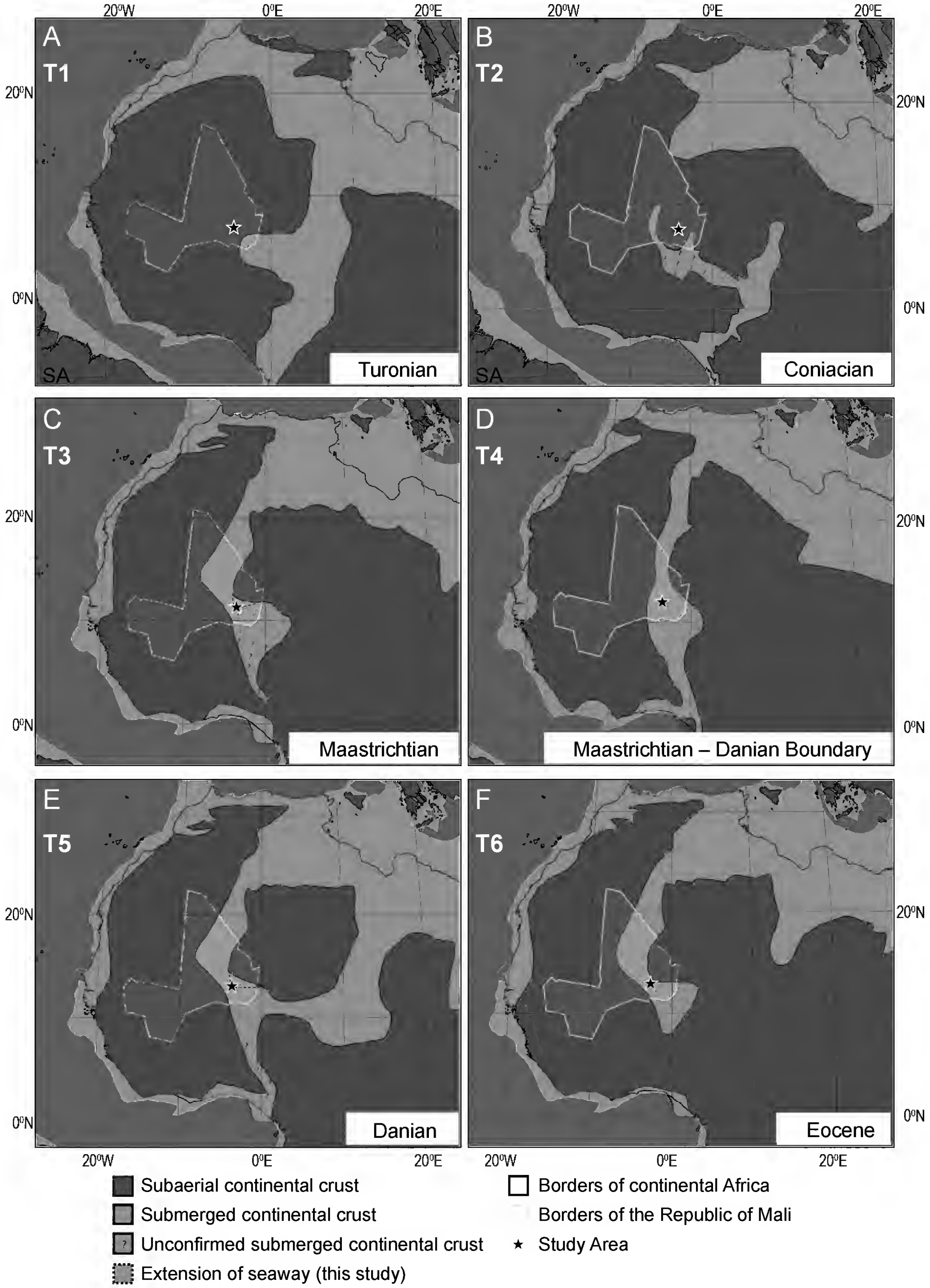
With regard to mollusks, about 350 specimens were collected from 10 of the localities that span the Late Cretaceous to Eocene. This collection consisted of a representative sample of the taxa present at each outcrop (not a bulk or systematic collection), thus the rarity or commonness of taxa cannot be inferred. Generally, we collected the best-preserved specimens we found. The mollusk fauna is often preserved as internal molds, occasionally as external casts and sometimes as the shell itself or a combination of these. Specimens are weathered and in poor condition and occasionally compressed and distorted. Nonetheless, family and sometimes generic and species identifications have been possible (see below). Most bivalves are articulated, suggesting rapid burial after death. Because interior shell structures such as hinges, teeth, and muscle scars have not been examined for articulated specimens, many bivalve identifications are to the family level only.

GPlates Reconstruction of the Trans-Saharan Seaway

The translation of field-based geological observations into maps of the Trans-Saharan Seaway has been attempted for over 50 years by numerous authors mentioned in the Introduction who created these maps by hand (e.g., Adeleye, 1975; Kogbe et al., 1976; Petters, 1977; 1979; Reyment, 1979; 1980; Kogbe, 1981; Boudouresque et al., 1982; Adetunji and Kogbe, 1986; Reyment and Dingle, 1987; Bellion et al., 1989; Kogbe, 1991; Damotte, 1995). Intervals of maximum transgression may have lasted only 10,000 years (Reyment, 1986), and whether the sea constituted a full north-south connection at different times has been debated by those same authors.

In Tapanila et al. (2008) we presented our hypothesis that six cyclothems (T1–T6) characterized the sedimentary record of northern Mali from the Late Cretaceous through the Early Paleogene. A cyclothem is a full cycle of sea-level rise followed by a disconformity marking a rapid sea-level fall. These events would have been third-order eustatic changes that would likely have been global in nature. To create an improved estimate of the extent of the Trans-Saharan Seaway through time we here apply GPlates, a computer-generated plate tectonic model (Boyden et al., 2011), to build maps that show the coverage of the Trans-Saharan Seaway from the Late Cretaceous to the middle Eocene. We manipulated the GPlates models for several time periods to reflect the data we have collected ourselves or integrated from generalized regional literature for central West Africa.

Methods: Within the open-source software GPlates, we consider a dataset of rotation and geometry files derived from information in several integrative research papers on tectonics (Seton et al., 2012; Matthews et al., 2016; Müller


A
T1
Turonian
SA
B
T2
Coniacian
SA
C
T3
Maastrichtian
D
T4
Maastrichtian – Danian Boundary
E
T5
Danian
F
T6
Eocene
20°W
0°E
20°E
20°N
0°N
Subaerial continental crust
Submerged continental crust
Unconfirmed submerged continental crust
Extension of seaway (this study)
Borders of continental Africa
Borders of the Republic of Mali
Study Area

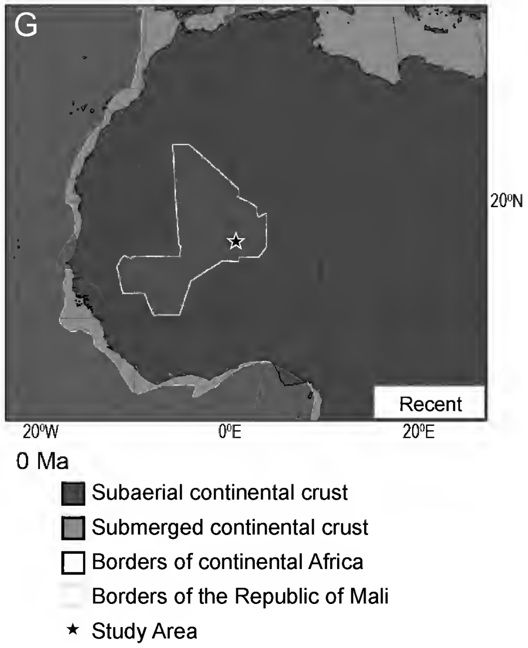


FIGURE 15 (*above and opposite page*). Our GPlates-based paleogeographic reconstructions of the Trans-Saharan Seaway in West Africa from the Late Cretaceous–early Paleogene (Boyden et al., 2011). Shorelines during six (T1–T6) cyclothems, or alternating marine and nonmarine sedimentary sequences, as described in the text. (*opposite page*) **A,** Turonian, modeled from Kogbe (1981), Reyment and Dingle (1987), and Meister and Piuz (2013); **B,** Coniacian, modeled from Reyment (1980) and Reyment and Dingle (1987); **C,** Maastrichtian, modeled from Guiraud et al. (2005) with minor additions from Adetunji and Kogbe (1986); **D,** Maastrichtian-Danian boundary, modeled from (Kogbe, 1981), Bellion et al. (1989) and Damotte (1995); **E,** Danian, modeled from Guiraud et al. (2005), with minor additions from Reyment (1980), and our new data; **F,** Eocene, based on information from Guiraud et al. (2005); and (*above*) **G,** Recent. The field area in Mali is situated within the tropics from the Turonian to the present day. Black star = locality Mali-17. SA = South America.

et al., 2016) to first establish a robust estimate of the positions of the continents at specific time points. These background data points provide up-to-date global plate tectonic reconstructions for the last 400 million years. With this data we used GPlates to model the positions of the present-day coastline and continental shelves, as well as a rotation spreadsheet that records the position and time-related rotation pole for each feature (e.g., continents) in the shape files (Matthews et al., 2016). Each feature is assigned a plate ID and each plate ID moves at the assigned rotation for a specified period. Any feature created and labeled with the same plate ID as West Africa will travel on the same tectonic rotation as West Africa and there is no relative movement between features with the same plate ID. The location of Africa at each age interval in figure 15 is derived from the research in Müller et al. (2016) on global plate boundaries and movements.

The modeling of the Trans-Saharan Seaway integrated data, such as facies analysis and mapping and localities of marine fossils, based on our own field observations from Mali and on publications that we cite below. We developed different methods for different time intervals to maximize the accuracy of the model at each of six intervals. Different models were necessary because some publications that focused on particular intervals provided better reference frameworks than others, which, in turn, could lead to more precise reconstruction in certain cases.

For example, where possible, the Trans-Saharan Seaway was modeled using data from Guiraud et al. (2005) because the paleogeological maps of West Africa those authors provided included a grid of lines of latitude and longitude every 5°. By matching the graticules, or grid squares, in GPlates to the same grid size of Guiraud et al. (2005), and drawing square by square, we aimed to produce a more accurate representation of the maximum transgression at a given time. This approach was not, however, possible for three of the six time periods. Thus, with an approach similar to the grid method we followed with the Guiraud et al. (2005) data, we created our GPlates model of the Trans-Saharan Seaway for these three periods using the seaway location within the borders of different countries as described by Kogbe (1981) and Damotte (1995). The latter method meant obtaining x-y coordinates of different points describing the seaway based on the adjacent coastline map from Reyment (1980) and Reyment and Dingle (1987). Based on our observations of marine fossils from several locations in northeastern Mali, we made small additions to the reconstruction of the Trans-Saharan Seaway for the Maastrichtian and into the Paleocene. Once the location of the seaway was modeled for each of the six time intervals, the seaway was assigned the same plate ID as West Africa in the GPlates program. Using GPlates, we then took snapshots of each of the different ages (fig. 15) to indicate the location of the seaway superimposed over the paleogeographic location of West Africa. Because the underlying data for this GPlates assessment are scaled to periods and epochs rather than to a numerical timescale, we carry this same temporal framework into our results (i.e., we do not provide numerical ages for the maps).

Results and Discussion: The results from GPlates generally resemble those in previously published maps, however; our new snapshot maps provide improved reconstructions for Mali, one of the most inland reaches of the ancient sea (fig. 15). Our interpretation varies slightly from prior reconstructions (Reyment, 1979; 1980; Boudouresque et al., 1982). Beginning in the Turonian, our maps show the transgressions starting out on a more easterly course through West Africa. Later, due to the impact of tectonics, the seas traveled west of the central Precambrian massifs. Finally, the northeasterly arm of the sea returned in the Paleocene. Our locality Mali-17 (starred on fig. 15) is noteworthy in being one of the most geographically internal marine fossil-producing localities in West Africa at this time. Intervals of maximum transgression are hypothesized to have lasted approximately 10,000 years (Reyment, 1986).

T1 Cyclothem: Cenomanian-Turonian (fig. 15A). Reyment (1979; 1980) argued that the first of the transgressions resulted in a north-south interconnection between the invading seas, but he considered the possibility of a connection through the Tilemsi Valley in Mali unresolved. He also considered this transgression to have been the equivalent of the North American Greenhorn cycle. Bellion et al. (1989) documented evidence of extensive gypsiferous deposits (indicating shallow, hypersaline embayments) and carbonates of Cenomanian-Turonian age in parts of the Tilemsi Valley and areas further west in the Taoudenit Basin, but did not establish whether there was a full link between the Tethys and south Atlantic (Gulf of Guinea) at this time. Kogbe et al. (1976: fig. 4) argued for a full north-south Trans-Saharan Seaway connection between the Tethys and the Gulf of Guinea in the Turonian that went through the "Niger valley" (p. 243) and not via the Benue Trough as was argued by Furon (1935).

Our modeling for the Turonian snapshot is based primarily on Kogbe (1981) and Reyment and Dingle (1987). Importantly, our Turonian snapshot does not show any seas within the Tilemsi Valley or the Gao Trench; north-south continuity was established through the Iullemmeden Basin in the eastern part of Mali as well as in Niger. The sea was mostly concentrated in areas such as Niger, Chad, and Nigeria. This picture differs substantially from that shown in Reyment (1980: fig. 3) where the Tilemsi Valley is partly flooded and the Gao Trench fully flooded.

T2 Cyclothem: Coniacian (fig. 15B). The second of the transgressions, considered to be the equivalent of North America's Niobrara cycle, was hypothesized to have been less extensive such that the embayments from the Tethys and the Gulf of Guinea did not connect (Reyment, 1979; 1980). Our modeling snapshot was based on Reyment (1980) and Reyment and Dingle (1987), and our results very closely resemble those of Reyment (1980: fig. 5). Our snapshot is noteworthy in showing that the seawater entering the Tilemsi Valley and Gao Trench in Mali had come from the south. The model is particularly poorly established for parts of Niger.

T3 Cylclothem – Campanian to Maastrichtian (fig. 15C). As many as three transgressions of the Trans-Saharan Seaway have been hypothesized during the Maastrichtian. Later transgressions, T4 (fig. 15D) and T5 (fig. 15E), have been the primary focus of our work, as these are the sediments that yielded important vertebrate fossils (Hill et al., 2008; Tapanila et al., 2008; Claeson et al., 2010). Because of the closure of the Benue Trough as a potential passage for continental seas, Reyment (1979; 1980) argued that the transgression that started in the Campanian became epicontinental only in the Maastrichtian and necessarily took a relatively western route across West Africa compared to earlier transgressions (Reyment, 1980). Specifically, this meant a route west of the Hoggar Massif (see also fig. 1B, C), an elevation of Precambrian rocks in Algeria (Krasheninnikov and Trofimov, 1969; Reyment, 1979: 32). Reyment (1980: 314) emphasized that it was "structural depressions" that were filled by the Maastrichtian and Paleocene transgressions but that the sea also overlay "stable craton" in places. Reyment (1979) also indicated that even though the Maastrichtian sea was extensive, there was little biostratigraphic evidence to support a full north-south Maastrichtian connection between the Saharan regions like Mali and basins adjacent to the Gulf of Guinea. Other authors suggested, based on fossil invertebrates, including bivalves and "free-swimming" ammonites, that the water could be characterized as fully marine into the Iullemmeden Basin in Niger and far from the open ocean (Moody and Sutcliffe, 1990: 21). Adeleye (1975) argued for a full connection at this time via the Niger Valley through Nigeria, Niger, and Sudan. Adetunji and Kogbe (1986) supported this inference, based on the discovery of the ammonite *Libycoceras* in Niger and southern Nigeria as well as similarities among ostracods in the two places (citing Kogbe, 1979). This idea stands in contrast to hypotheses of Petters (1977; 1979) who argued that the northern marine incursion terminated as an embayment because the foraminiferans are very different in the Sokoto area than in southern Nigeria. Adetunji and Kogbe (1986), however, suggested that this difference could be simply a local environmental variation. The case for a full Maastrichtian connection was also proposed on the basis of vertebrates, specifically mosasaur species, found to be present in Niger and in Nigeria (Lingham-Soliar, 1998).

Our modeling is based on the work of many previous authors, including Reyment (1980) and Guiraud et al. (2005), with minor additions from Adetunji and Kogbe (1986). Although much fieldwork remains to be done, our tectonically informed Maastrichtian snapshot shows a full sea connection through the Tilemsi Valley, Gao Trench, and Iullemmeden Basin. In contrast to the Coniacian, this sea came into Mali from the north. This sea also linked to a large embayment that spread into neighboring Niger. Our model does not show a full southern sea connection in the Maastrichtian, but instead, several areas of unconfirmed marine coverage with the ocean tapering out just short of a full connection to the Gulf of Guinea, similar to estimates by Guiraud et al. (2005: fig. 49B).

T4 Cyclothem: Maastrichtian-Danian Boundary (fig. 15D). Damotte (1995: fig. 1) studied ostracods from North Africa (northern Algeria and Tunisia), south through Mali (Tilemsi Valley, near Tichet), and continuing south to the Congo and concluded that there was a fully connected Trans-Saharan Seaway during the late Maastrichtian-Paleogene transgression. He stated that this conclusion, supported by the work of Reyment and Dingle (1987) derived from the marine nature of the ostracod fauna. Kogbe (1981), Bellion et al. (1989) and Damotte (1995), and Guiraud et al. (2005), with minor additions from Reyment (1980), were the primary sources for our snapshot at the Maastrichtian-Danian boundary (~ 66 Ma). Our model shows a full north-south connected seaway close to the K-Pg boundary.

T5 Cyclothem: Danian (fig. 15E). In the Paleogene various authors reconstructed the Trans-Saharan Seaway as fully connected, linking the Tethys and Guinean Seas (e.g., based on ostracod species distribution sensu Reyment, 1980; Kogbe, 1981; Bellion et al., 1990: fig. 1). An alternative model reconstructs two separate, disconnected gulfs: the Tethys Sea inundating West Africa from the north, with shallow, warm, and hypersaline waters, and the Guinean Sea, encroaching from the south, bringing poorly oxygenated waters with low salinity (Petters, 1977: figs. 6–9; 1979; Boudouresque et al., 1982). Important tectonic variables impacting the late Paleocene (and subsequently early Eocene) sea-level rise may have been both higher oceanic crust production and the emergence of the oceanic ridge that formed as Norway separated from Greenland (Miller et al., 2005). Adeleye (1975) argued against a connection through the latest Paleocene, as did Petters (1977) based on differences in the microfaunas of northwestern Nigeria versus the southern Nigerian Sedimentary Basin. Reyment (1979) rebutted this claim, specifically noting extensive similarities among the Paleocene ostracod faunas from Libya, Mali, Niger, and Nigeria. He argued that the 600 km break in the continuity of outcrops may simply have been due to erosion rather than lack of sedimentation in the sea's absence. Nautiloids from Niger have also been used to support a fully connected Trans-Saharan seaway (Tintant et al., 2001) in the Paleocene. Petters (1977) argued for a maximum extent of the Trans-Saharan Seaway in the latest Paleocene, where he hypothesized that the sea had a southern reach well into northern Nigeria from the north. Boudouresque et al. (1982) corroborated this finding in a study of palynology.

Kogbe (1981), Bellion et al. (1989), Damotte (1995), and Guiraud et al. (2005), with minor additions from Reyment (1980), were the sources for our Danian snapshot. It supports the hypothesis that the Trans-Saharan Seaway formed a continuous link between the Tethys and the South Atlantic at times during the Paleocene. Phosphatic shales and conglomerates become part of the cyclothem-succession package near the top of a transgressive-regressive cycle. Our full north-south connection is qualified by some poorly confirmed areas in Nigeria. We also found a separate marine incursion in the east that would have passed through Niger and Chad, isolating the exposed Precambrian basement rocks of the Hoggar, Aïr, and Adrar des Iforas massifs as an island. The maximum continental flooding of Cyclothem 5 occurred in the mid-Paleocene (Reyment, 1979).

T6 Cyclothem: Eocene (fig. 15F). In their study of neritic ostracods of the Tethys, Speijer and Morsi (2002: fig. 1) showed full connection of the Trans-Saharan seaway at the PETM, an interval during which sea level rose ~ 20 m in less than 100,000 years (Speijer and Wagner, 2002). Guiraud et al. (2005: fig. 57B) argued that substantial sea coverage of West Africa continued into the early-middle Eocene, with water extending into Mali from the North and flooding the Tilemsi Valley, Gao Trench, and part of the Iullemmeden Basin. In our model, which is based heavily on the work of Guiraud et al. (2005), no connection persists between the Trans-Saharan Seaway and the Gulf of Guinea. The presence of the same species of pycnodont fish *(Pycnodus bowerbanki)* in rocks of the Iullemmeden Basin and rocks of the London Clay was suggested as a reason to support some migration between ocean waters around Europe and those within west Africa via the Trans-Saharan Seaway as late as the Lower Ypresian part of the Eocene (Moody and Sutcliffe, 1990). Nonetheless, by the Paleocene and especially the early-middle Eocene, the depositional environment in Mali had likely become very shallow and verged on isolated, most likely brackish and even occasional fresh water embayments cut off from the retreating Trans-Saharan Seaway. The seaway that had receded northward by this time had begun to close permanently, and the large embayment seen in Mali could have been entirely cut off from the main Trans-Saharan Seaway. This hypothesis is reinforced by the presence of both freshwater and saltwater fish species present at this time, as we discuss below.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Thalassinoides* Ehrenberg, 1944

Figure 16

Horizons in Study Area and Age: Tichet and Ménaka formations of the Taoudenit Basin and Teberemt Formation of the Gao Trench. Campanian to Paleocene

Localities: Mali-1, Mali-3/4, Mali-17, Mali-18, Mali-19.

Depositional Environment: Sandstones and siltstones (Facies 1), indicating tidally influenced shoreline and deltaic environments; marl and shale (Facies 4), indicating shallow, sublittoral, open marine settings with water depths <50 m; and phosphate conglomerate (Facies 5), indicating shallow marine-to-brackish water phosphorites.

Referred Material: Field photo only (fig. 16).

Description: Boxwork burrow system with Y-shaped branches and passive fill. Burrows are typically 1–2 cm in diameter, and sometimes enlarged with iron oxide concretions up to 4 cm in diameter. Specimens occur in very fine sandstone, silt, and phosphate conglomerates.

Discussion: *Thalassinoides* is a common Phanerozoic ichnogenus interpreted as a structure made by decapod crustaceans, a conclusion supported by associations of crustacean body fossils with *Thalassinoides* (de Carvalho et al., 2007). We observed *Thalassinoides* firmgrounds in close association with phosphatic conglomerates (Facies 5) at Paleocene localities Mali-18 and -19 (Tapanila et al., 2008). Moody and Sutcliffe (1990: 22) observed the possible presence of this taxon but did not figure or formally describe it, noting only that it characterized Paleocene rocks of the Iullemmeden basin in Niger. Myrow (1995) described *Thalassinoides* as common in intertidal and marginal marine facies.

Ichnospecies *Teredolites clavatus* Leymerie, 1842

Figure 5

Horizon in Study Area and Age: Tichet Formation of the Taoudenit Basin. Campanian.

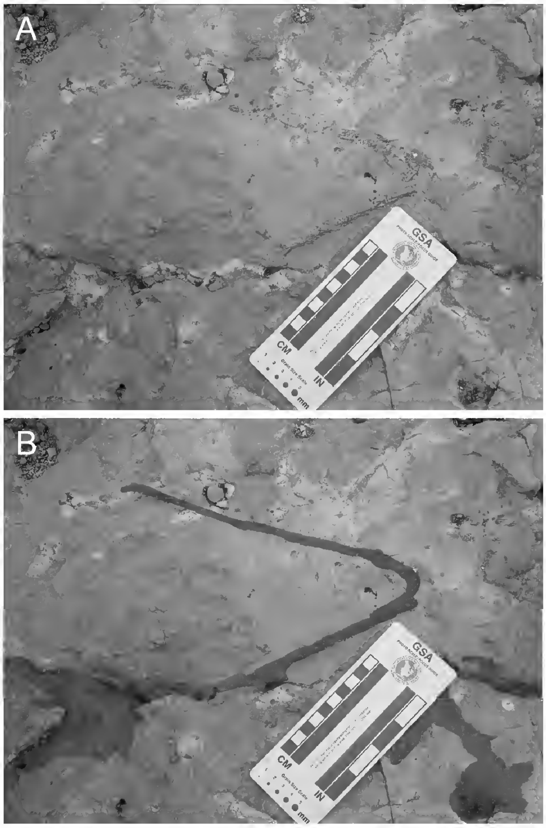


FIGURE 16. The ichnogenus *Thalassinoides*, a network of burrows often with Y-shaped branching, possibly made by decapod crustaceans. **A,** field photo of burrows in situ in a sandstone (Facies 1) at the base of either locality Mali-17 or -18, Paleocene of the Teberemt Formation, Gao Trench; **B,** burrows highlighted for clarity.

Locality: Mali-4 unit 1, 16 m from base.

Depositional Environment: Sandstone (Facies 1), indicating tidally influenced shoreline and deltaic environments.

Referred Material: CNRST-SUNY 134.

Description: Round- to club- or flask-shaped cavities within fossil wood that have been infilled by sand matrix. Cavities are tightly packed, but distinct from each other and distributed within a substrate that has regular ridges. Diameter of borings is 4–6 mm.

Discussion: *Teredolites* are borings produced in woody substrates (Bromley et al., 1984). The borings tend to be clavate (i.e., sock shaped with a swollen internal end that tapers toward an aperture). The regular ridges observed here suggest a preservation of the internal structure of the wood. This ichnofossil is made by pholadid bivalves. *Teredolites*, differs from another bivalve trace fossil, *Gastrochaenolites*, because the latter's borings (described below) penetrate lithic substrates (Kelly and Bromley, 1984). The Malian specimens compare closely with published images of *Teredolites clavatus* (Bromley et al., 1984). Wood-boring pholadid bivalves excavate and live inside driftwood, an invertebrate behavior that extends back at least to the Jurassic period (Kelly, 1988). These bivalves are suspension feeders and do not derive nutrition from the wood itself (Carmona et al., 2007). Fossilized wood is not particularly abundant in the Malian section, and so the wood sample with *Teredolite*s provides an important record of an otherwise unpreserved terrestrial flora, a more general pattern discussed by Savrda (1991).

Ichnospecies *Gastrochaenolites ornatus* Kelly and Bromley, 1984

Figure 17

Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin, Teberemt Formation of the Gao Trench, and the Tamaguélelt Formation of the Taoudenit Basin. Maastrichtian-Eocene.

Localities: Mali-8 unit 10; Mali-18 units 2 and 5; Mali-19 units 2 and 5; Mali-20 units 2 (the "lower phosphate," also called "Mali-20a" by McCartney et al., 2018), 4 and 7.

Depositional Environment: Phosphatic conglomerates (Facies 5), indicating shallow marine-to-brackish water phosphorites, specifically, cobblegrounds composed of coprolites, bone fragments, and phosphatized nodules.

Referred Material: Our collection contains numerous fossil coprolites, bones, and phosphatic clasts with borings (Tapanila et al., 2004). Examples include: coprolites: CNRST-SUNY $184^{8\text{-unit } 10}$, $200–246^{20\text{-unit } 2}$, fish bone $247–254^{20\text{-unit } 2}$, and phosphatic clasts $256–258^{19 \text{ unit } 2}$.

Description: Flask-shaped borings in lithoclasts, coprolites, and fossilized bone.

Discussion: Our Malian fieldwork and analysis yielded the first described occurrence of bivalve borings in coprolites and their oldest occurrence in fossil bone (Tapanila et al., 2004). Tapanila et al. (2004; 2008) figured and described several examples of *Gastrochaenolites*, flask-shaped borings in lithified bone, coprolites, and lithoclasts. Tapanila et al. (2004) recognized that the tracemaker left an external mold allowing the animal to be identified as a pholadid bivalve and member of Martesiinae. This observation was the first record of rock-boring bivalves from the Paleocene of West Africa and the oldest known record of this ichnospecies.

Functionally, the bivalve has been hypothesized to have been able to penetrate the lithic substrate using mechanical means, essentially grinding the substrate with its shell (Tapanila et al., 2004). The bivalve then matures and lives in the protective hole as the animal subsists on suspension feeding from circulated water. Tapanila et al. (2004) observed differences in the relative shapes of *Gastrochaenolites* in fossil bone versus those in coprolites, with the openings in coprolites having a more pronounced flask shape (i.e., a broad base and narrow surface opening). The presence of pholadid bivalves is an important environmental indicator. These species inhabit normal marine water thus their presence suggests that the localities that yielded these fossils were under normal marine salinity, at least at some point. Malian rocks contain both lithic and xylic burrowers, and physical protection may have been part of the need to burrow into lithified substrates. Below we note further examples of *Gastrochaenolites* in the bone of pycnodont fishes.

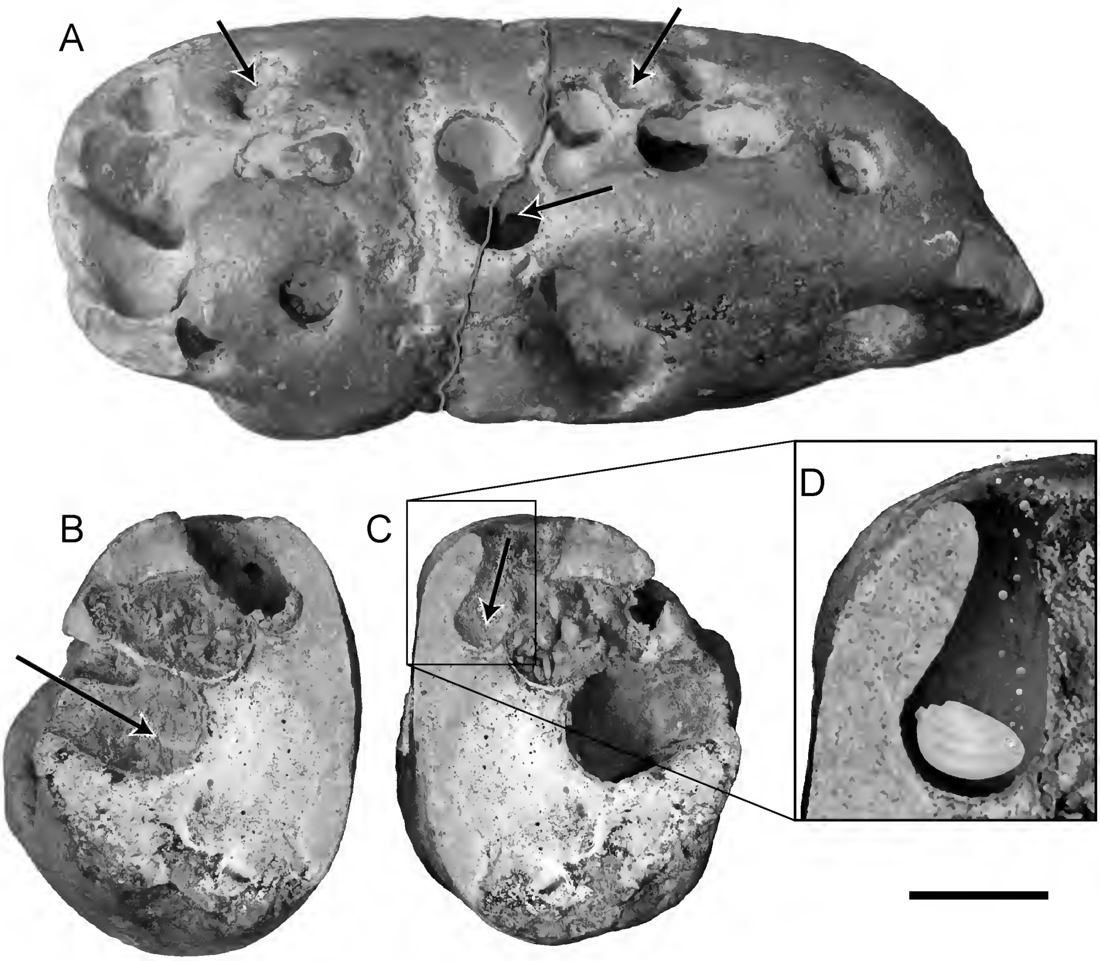


FIGURE 17. The ichnospecies *Gastrochaenolites ornatus* (arrows) within a vertebrate coprolite (CNRST-SUNY 215) from the lower phosphates of Mali-20, Eocene of the Tamaguélelt Formation, Taoudenit Basin. **A,** coprolite with numerous burrows, jagged red line indicates site of break; **B,** open left, and **C,** open right, surfaces showing the characteristic flask shape of burrows in cross section. **D,** life reconstruction of the pholadid bivalve (subfamily Martesiinae) based on the external mold described in coprolite CNRST-SUNY 206 from the same locality, showing how these filter-feeding animals were situated in their burrows in life. We hypothesized that the pholadid in CNRST-SUNY 206 was a 2–3 year old member of either *Penitella* or Pholadidae (Tapanila et al. 2004). See also figure 57 for an example of *Gastrochaenolites ornatus* in vertebrate bone. Scale bar = 1 cm.

Ichnogenus *Skolithos* sp. Haldeman, 1840

Figure 4D

Horizons in Study Area and Age: Tichet Formation of the Taoudenit Basin. Campanian-Maastrichtian.

Localities: Mali-1 and Mali-3.

Depositional Environment: Sandstone delta deposit (Facies 1), indicating tidally influenced shoreline and deltaic environments.

Diagnosis: Tube- or pipe-shaped structures 3–5 cm long.

Referred Material: Burrows were not collected but documented in a field photo.

Description: Tube-shaped sandstone forms that are oriented vertically.

Discussion: *Skolithos* are common trace fossils of shallow marine environments, which in the Mali sections are observed in sandstones, including those that contain climbing ripples. This geological setting suggests a lower flow regime and high-sediment supply common to delta deposits. It has generally been hypothesized that worms made the traces as burrows (Barwis, 1984).

COPROLITES

Morphotypes 1–5 Tapanila et al., 2008

Figures 17–19

Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin, Tamaguélelt and Teberemt formations of the Gao Trench and Tamaguélelt Formation of the Taoudenit Basin. Maastrichtian-Eocene.

Localities: Mali-8 unit 10; Mali-16 unit 4; Mali-18 and -19 units 2 and 5; and Mali-20 units 2, 4, and 7.

Depositional Environment: Phosphatic conglomerate (Facies 5), indicating shallow marine-to-brackish water phosphorites, amalgamated and concentrated by storm activity, shallow marine to brackish water environment between fair weather and storm-wave base (Tapanila et al., 2008).

Referred Material: From locality Mali-20, the following morphotype exemplars have been identified and illustrated here: CNRST-SUNY 564A, 565A, 566A, 567A, 568A, and 569. There are over 100 more coprolites in the collection, primarily from Mali-20 that are batch-cataloged under the numbers CNRST-SUNY 184–85, 200–246, 610–619, 621, 623–626, 629, 634, 636–647, and 649–674.

Description: These are cylindrical phosphatic clasts that differ from lithoclasts in their consistently elongate form (typically oblate ovoid), and their external sculpture of spiraling or longitudinal furrows. The internal composition of the coprolites is typically very fine-grained phosphomicrite that is mottled in color with occasional bioclasts including fish vertebrae and moldic shells. All phosphate conglomerate units of our composite section yield vertebrate coprolites and we recognized five coprolite types that have been recovered from these Malian localities (Tapanila et al., 2008). Three of the coprolite types are spiral: Type 1 (wide, amphipolar; dextral; 80–350 mm; e.g., CNRST-SUNY 568A); Type 3 (narrow, amphipolar; sinistral; 5–9 mm; e.g., CNRST-SUNY 566A); and Type 5 (heteropolar; sinistral; 60–200 mm; CNRST-SUNY 564A). The remaining two types are straight: Type 2 (wide; 100–350 mm; e.g., CNRST-SUNY 567A) and Type 4 (narrow; 5–9 mm; CNRST-SUNY 565A).

Discussion: The producers of the coprolites are mostly unknown, but the size range and morphologies can be linked to vertebrate species from among the varied taxa preserved in the Malian fossil fauna. Tapanila et al. (2008) attributed the spiral coprolites (types 1, 3, and 5) to three different nonteleost, carnivorous fish, for example, batoids, sharks, amiids, or dipnoans. Those taxa have spiral-shaped intestinal valves that are thought to have created the distinct markings on coprolites (Neumayer, 1904; Jain, 1983). In particular, Type 5 coprolites have an asymmetric spiraling suggesting they may be gut contents (enterospirae) and not feces that had been expelled from

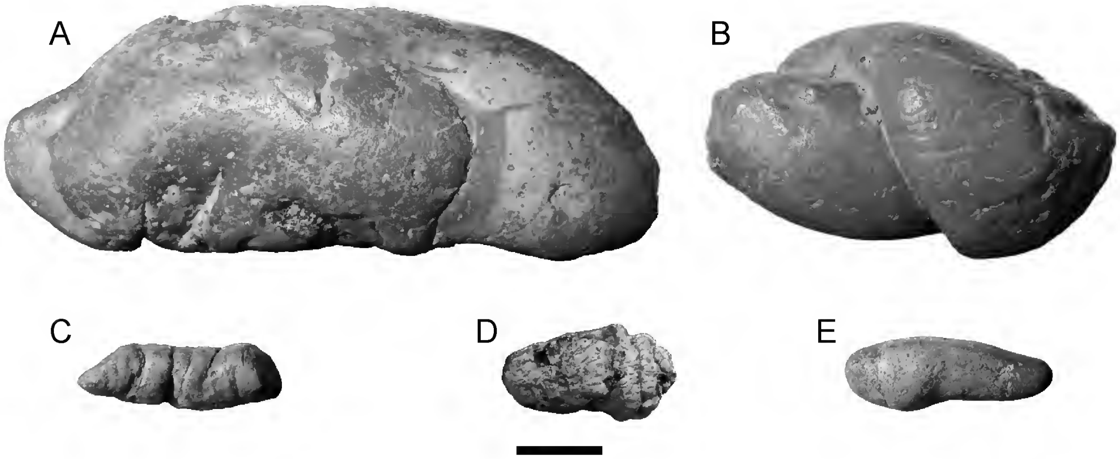


FIGURE 18. Examples of five vertebrate coprolite types identified from phosphatic deposits of Mali-20, Eocene of the Tamaguélelt Formation, Taoudenit Basin (Tapanila et al., 2008). **A,** Type 2, wide and straight, spiral absent (CNRST-SUNY 567A); **B,** Type 1, wide and amphipolar with a dextral spiral (CNRST-SUNY 568A); **C,** Type 3, narrow and amphipolar with sinistral spiral (CNRST-SUNY 566A); **D,** Type 5, heteropolar with sinistral spiral (CNRST-SUNY 564A); and **E,** Type 4, narrow and straight, spiral absent (CNRST-SUNY 565A). Scale bar = 1 cm.

the animal (e.g., sharks) in life. Tapanila et al. (2008) concluded that there was insufficient evidence to specify vertebrate producers for the straight coprolites. Fish bones and molds of what appear to be crustacean shells were found in a random sampling of the larger coprolites (types 1 and 2; see fig. 19).

Ichnospecies *Linichnus serratus* (Jacobsen and Bromley, 2009)

Figure 20A

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-8 unit 10.

Depositional Environment: Phosphatic conglomerate (Facies 5), indicating shallow marine-to-brackish water phosphorites amalgamated and concentrated by storm activity, shallow marine to brackish water environment between fair weather and storm-wave base (Tapanila et al., 2008).

Referred Material: Located on postcranial elements of dyrosaurid crocodyliforms: CNRST-SUNY 285, 286, 287, 335.

Description: Feeding traces on four isolated crocodyliform bone fragments, consisting of straight, parallel grooves with a U-shaped cross section, approximately 1 mm wide and 1 mm deep (Hill et al., 2015).

Discussion: Jacobsen and Bromley (2009) diagnosed *Linichnus serratus* as encompassing single elongate grooves of biogenic origin on skeletal material; U- or V-shaped in transverse section. The depth of individual traces may affect only the bone surface or may cut more deeply disrupting bone fibers.

The feeding traces present on bones in the current sample include long grooves with U-shaped cross sections. Some are assembled in parallel or subparallel groupings; however, each trace was likely made by the apex of an individual tooth. The traces were described in detail and attributed to postmortem or perimortem feeding by sharks on dyrosaurids (Hill et al., 2015).

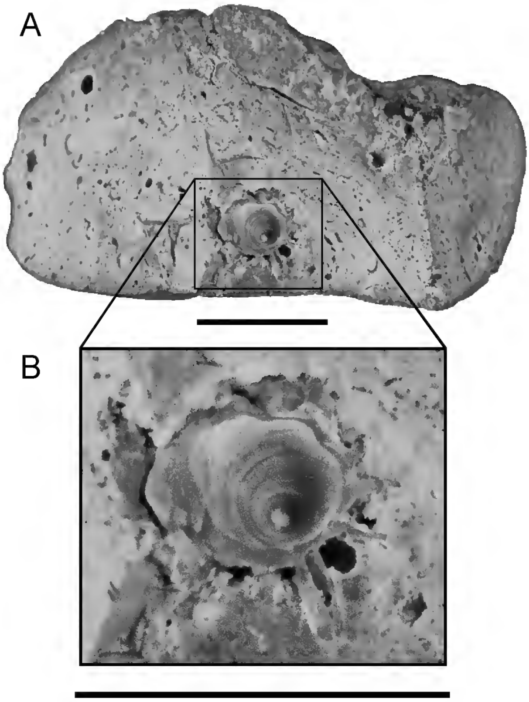


FIGURE 19. Type 2 vertebrate coprolite. **A,** Internal view of broken coprolite (CNRST-SUNY 569) from the phosphatic conglomerates of Mali-20, Eocene of the Tamaguélelt Formation, Taoudenit Basin, showing fish vertebra; **B,** vertebra enlarged. Scale bars = 5 mm.

Ichnospecies *Knethichnus parallelum* Jacobsen and Bromley, 2009

Figure 20B

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-8 unit 10.

Depositional Environment: Phosphatic conglomerate (Facies 5), indicating shallow marine-to-brackish water phosphorites amalgamated and concentrated by storm activity, shallow marine to brackish water environment between fair weather and storm-wave base (Tapanila et al., 2008).

Referred Material: Isolated vertebral centrum from a dyrosaurid crocodyliform, CNRST-SUNY 335.

Description: Feeding traces consisting of closely spaced, parallel grooves, on an isolated crocodyliform vertebral centrum.

Discussion: Jacobsen and Bromley (2009) diagnosed this ichnogenus as scraping structures in which serration traces extend as parallel grooves leading in some cases away from an initial groove. The current specimen is a single vertebral centrum, likely pertaining to a dyrosaurid, that bears a variety of feeding traces, including some referable to *Knethichnus parallelum.* They consist of closely spaced, parallel grooves that were likely formed by dragging the denticles of a serrated tooth. Similar traces are known to have been made by *Squalicorax* sharks (Schwimmer et al., 1997). Despite the absence of dental remains, this trace fossil provides evidence of serrate-toothed sharks in the Maastrichtian Trans-Saharan Seaway (Hill et al., 2015). Because both sharks and dyrosaurids fall into the apex predator category within the ancient ecosystem, the case we have reported is noteworthy in preserving the feeding of one apex predator on another (fig. 20C, D).

SYSTEMATIC PALEONTOLOGY

ANGIOSPERMAE Lindley, 1830

FABACEAE Lindley, 1836

CAESALPINIOIDEAE de Candolle, 1825

?*Caesalpinioxylon moragjonesiae* Crawley, 1988

Horizon in Study Area and Age: Most likely Teberemt Formation of the Gao Trench. Middle-Upper Paleocene.

Locality: Samit Region, 199 km NE of Gao (Crawley, 1988: 5).

Depositional Environment: Limestone and calcareous marl (Crawley, 1988); specimen not collected by us but probably from our Facies 4, based on published description, and thus a shallow, sublittoral open marine setting with water depths <50 m.

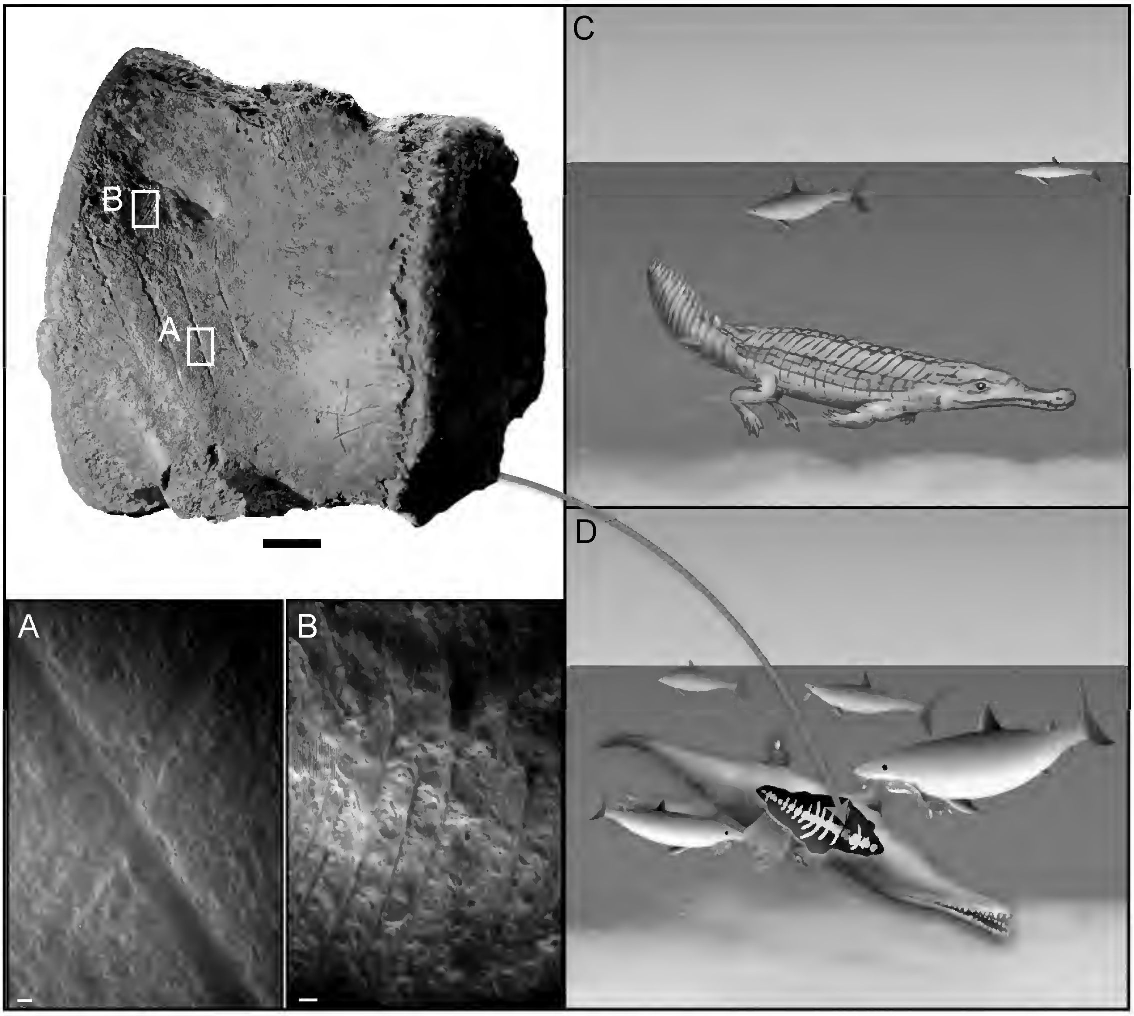
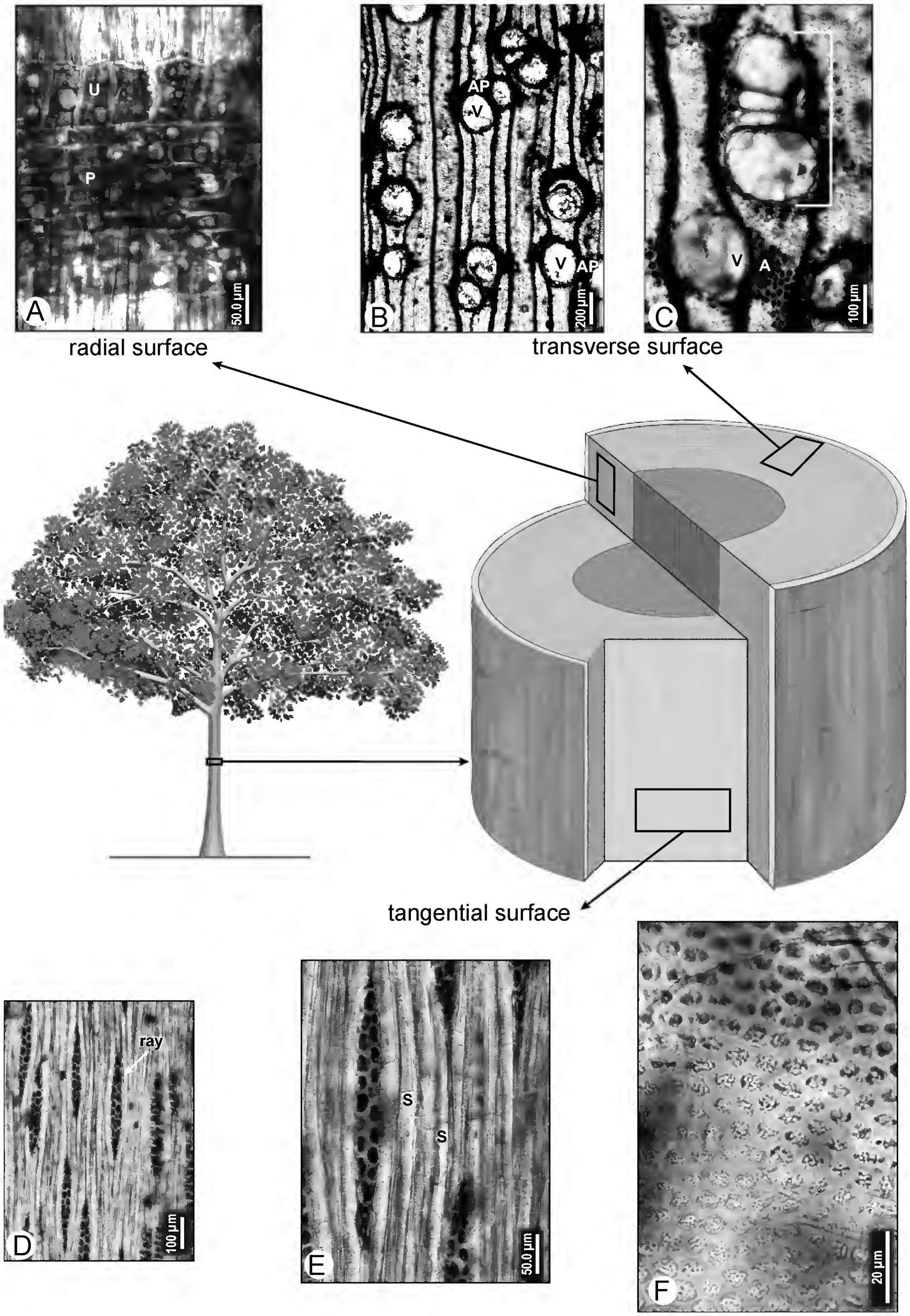


FIGURE 20. Reconstruction of multispecies shark feeding on a dyrosaurid crocodyliform as interpreted from ichnofossils. Ichnofossils on a dyrosaurid vertebral centrum (CNRST-SUNY 335) in right lateral view (ventral to top of image) from phosphatic deposits of Mali-8 (unit 10), from the Maastrichtian of the Ménaka Formation. The bone records the feeding behavior of at least two different species of sharks. **A,** ichnospecies *Linichnus serratus*, scanning electron micrograph denoting feeding trace left by the apex of a single tooth. **B,** ichnospecies *Knethichnus parallelum*, scanning electron micrographs showing closely spaced, parallel marks left by a tooth with closely spaced denticles. **C–D,** sharks and dyrosaurids were apex predators in the Trans-Saharan Seaway, but larger sharks may have attacked living dyrosaurids, dismembering and eviscerating the carcass, whereas smaller sharks likely scavenged on the remains and could access deeper body regions near the vertebral column. Scale bar for vertebra = 1 cm; for A and B = 200 μm.


U
P
50.0 µm
A
AP
V
V
AP
200 µm
B
V
A
100 µm
C
radial surface
transverse surface
tangential surface
ray
100 µm
D
S
S
50.0 µm
E
20 µm
F

Referred Material: NHMUK PB V.62187, V.62188.

Description: See Crawley (1988).

Discussion: Although we did not collect these fossils, we note them again here because they are an important and rare record indicating that wood fossils from the Paleocene near Samit belong to Fabaceae, subfamily Caesalpinioideae (Crawley, 1988). This clade, which is still extant, has a predominantly tropical distribution and is particularly good at colonizing disturbed habitats, or those subject to short term and naturally occurring change induced by factors such as flooding (Herendeen et al., 1992). A significant feature of these specimens is that they contribute primary evidence that lowland tropical rainforest was present across the Sahara from the Cretaceous through the Paleocene as part of a "South America–Africa floristic region" (Axelrod and Raven, 1978: 86–87; 117). According to these authors "local montane areas in the inner tropics were clothed with rainforests" at this time (Axelrod and Raven, 1978: 117).

FABACEAE Lindley, 1836

Figure 21

Horizon in Study Area and Age: Middle Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Chalky, micritic limestone with thin shale partings (Facies 3); low-energy, normal marine conditions.

Referred Material: CNRST-SUNY 576, 577, 578.

Description: Based on CNRST-SUNY 577. Growth rings not observed. Wood diffuse-porous. Vessels: solitary and in short radial multiples of 2 (-3); mean tangential diameters 167 (SD = 37) –192 (SD – 35) µm; 3–9 vessels per mm^2; perforation plates exclusively simple; intervessel pits crowded alternate, vestured, small, 5–6 (–7) µm horizontal diameter; vessel-ray pits similar to intervessel pits; average vessel element length 545 (SD = 89) µm. Axial Parenchyma: predominantly narrow vasicentric, sometimes aliform—confluent, tendency to unilateral paratracheal; strand length probably >4 cells. Fibers: thick walled, pits not observed, possibly both septate and nonseptate. Rays: mostly two cells wide, 10–14 cells high; uniseriate rays not common, <10 cells high. Storied structure: absent. Canals: absent.

Discussion: We first provide an overview of basic wood anatomy before discussing the Malian specimens. Wood (secondary xylem) of almost all nonmonocot angiosperms is a complex plant tissue with vessel elements (dead and hollow at functional maturity) for water conduction, and fibers (usually dead at functional maturity) for support. Both these cell types are oriented parallel to the long axis of a plant (i.e., an axial orientation). Rays composed of ray parenchyma cells extend from the bark to the center of the tree and are important for food storage, wound response,

FIGURE 21. Paleocene fossil wood specimens, Fabaceae (CNRST-SUNY 577), from Mali-17 (unit 3), Paleocene of the Teberemt Formation, Gao Trench. At center is an idealized reconstruction of the full tree in life (which may have been over 15 m in height) for orientation of fossil wood sections, and section of a tree trunk showing the orientation for cutting transverse, radial, and tangential sections. **A,** radial section showing detail of a ray with procumbent (horizontally oriented) cells (P) in the middle of the ray, and a single row of square-upright cells (U) at the margins; **B,** transverse section showing diffuse-porous wood with solitary vessels (V) rounded in outline, axial parenchyma (AP, cells with dark contents) associated with vessels concentrated on one side of vessel and with short wings (aliform); **C,** transverse section with radial multiple of four vessels (bracket) and solitary vessel (V) with diagnostic feature of aliform axial parenchyma (A); **D,** a tangential longitudinal section showing rays, mostly biseriate (two cells wide); **E,** tangential longitudinal section at higher magnification showing more details of biseriate rays, as well as fibers that are possibly septate, and septae (thin cross walls) above "S"; and **F,** alternate (diagonally arranged) intervessel pits (breaks in the cells wall to interconnect adjacent vessels) with vestures (outgrowths of the pit borders that appear as small dots).

and manufacturing chemicals that inhibit fungal and insect attack. Most trees also have some axial parenchyma. Parenchyma cells are living in the sapwood of a tree. The sizes, proportions, arrangements, and interconnections between these cell types vary among plant families and genera and are useful for their identification.

Because wood is an ordered tissue composed of longitudinally (axially) oriented and horizontally oriented cells, randomly placed cuts through a wood rarely yield useful information for determining nearest living relatives. It is necessary to make precisely cut sections in three different planes: transverse (cut across the longitudinal axis), tangential longitudinal (cut down parallel to outside surface of a tree), and radial longitudinal (cut down parallel to the rays' orientation, from outside of tree toward its center). These different planes expose different diagnostic features, e.g., transverse views expose vessel diameters, frequency, and arrangement. Tangential longitudinal section views expose ray width and height, and the breaks in the cell walls that serve as interconnections between vessels in a group, or "multiple" in botanical terminology. Radial sections are best for seeing both the end-to-end connections between the individual vessel elements (cells that are usually <1 mm long) forming vessels ranging in length from a few centimeters to more than 10 m, as well as to see ray cellular composition. The description of the Mali Paleocene wood uses terms from illustrated and standardized terminology (IAWA Committee, 1989).

The specimen CNRST-SUNY 577 is the best preserved of the three fossil wood samples, hence it is the basis for our description. CNRST-SUNY 576 and 578 likely represent the same tree type because they have similar vessel, parenchyma, and ray patterns. The slight differences observed in axial parenchyma abundance, vessel diameter, and frequency are comparable to variation found within a single modern wood species.

The multiple entry key of the online database InsideWood (Wheeler, 2011) was used to search for species with the combination of the features: vessels solitary and in short multiples that are randomly arranged, vestured alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, narrow rays with one marginal row of upright cells, and axial parenchyma associated with vessels. This general combination of features occurs in two families: Combretaceae and Fabaceae, both of which have species that today occur in or border mangrove swamps. Both families have an extensive fossil record (Gregory et al., 2009). While most genera of Fabaceae can be distinguished from genera of the Combretaceae, there is overlap in the wood anatomical characteristics of some genera. The scarcity of uniseriate rays in the Mali wood argues against affinities with the Combretaceae. As such these woods are tentatively assigned to Fabaceae.

These woods differ from *Caesalpinioxylon moragjonesiae* Crawley (1988) from the Paleocene of Mali as that wood has banded axial parenchyma and its rays tend to be storied (rays aligned in horizontal tiers as viewed in tangential sections). This new Malian wood also differs from seven other previously described Paleocene woods from Niger in West Africa, all of which have some form of banded axial parenchyma (Koeniguer et al., 1971).

None of the samples has growth rings, suggesting that, in life, there was no pronounced dormancy for the tree, and also suggesting an aseasonal environment. Carlquist (1975; 1977) proposed using the Vulnerability Index (V = mean tangential diameter/number of vessels per mm^2) as a means of expressing the riskiness of the hydraulic structure of a plant, i.e., the plant's susceptibility to developing embolisms and losing water conduction. Low V values (<1) as found in woods with many narrow vessels suggest a plant that can tolerate environments with water stress. A plant with high V values is one that is unlikely to survive in environments subject to drought or freezing. The Paleocene Mali woods have high V values suggesting the source trees did not experience water stress. The water-conducting vessels are wide in all three samples (table 3) and this suggests the source plants were trees with trunks at least 15 m tall (Wheeler et al., 2007; Olson et al., 2014).

TABLE 3

Vulnerability Index for fossil wood samples from Mali-17 unit 3 from the Paleocene of the Teberemt Formation.

Carlquist (1975, 1977) proposed using the Vulnerability Index (V = mean tangential diameter/number of vessels per mm^2) as a means of describing a plant's hydraulic structure. The relatively high V values in the specimens examined here suggest that the Paleocene fossil trees in Mali did not experience water stress, and further suggest that water was available year-round.

Sample	Tangential diameter	Vessels/mm^2	V value
CNRST-SUNY 576	192 (35) µm	6.7 (5–9)	28.75
CNRST-SUNY 577	184 (27) µm	5.3 (3–7)	34.77
CNRST-SUNY 578	167 (37) µm	5.2 (4–7)	32.12

ECHINODERMATA Bruguière, 1791

ECHINOIDEA Leske, 1778

SPATANGOIDA Agassiz, 1840

Linthia sudanensis Bather, 1904

Figure 22

HORIZON IN STUDY AREA AND AGE: Teberemt Formation of the Gao Trench, Taoudenit, and Iullemmeden basins. Paleocene.

LOCALITIES: Mali-3 unit 3; Mali-7 unit 15; Mali-16 unit 1; Mali-17 unit 3; Mali-18 unit 1, and Mali-19 unit 1.

DEPOSITIONAL ENVIRONMENTS: Limestone (Facies 3), open marine conditions.

REFERRED MATERIAL: The collection contains numerous specimens of this taxon. Exemplars include: CNRST-SUNY 72, 73, 75–76$^{7\text{-unit }15}$; 162 and 171$^{3\text{-unit }3}$; 570–571, 579–582, 602–603$^{16\text{-unit }1}$; 583$^{17\text{-unit }3}$. Some specimens pertaining to biostratigraphy were identified in the field and not collected.

DESCRIPTION: These irregular echinoids, a type of "heart urchin," typically measure ~3.5 cm wide at the ambitus (anterior to posterior), vary from 1–2 cm in height, and display an inflated, ovate test. The distinct frontal groove (the large indentation that forms the heart shape of the echinoid) is edged by large tubercles. The ambulacra are often well preserved. The anterior ambulacra are elongate and sunken, in contrast to the posterior ambulacra that are half the length and expressed more shallowly on the test. The peristome is widely gaping and kidney shaped, formed in part by the anterior margin of the labrum. The periproct is located well above the ambitus.

DISCUSSION: *Linthia* is a common infaunal genus of the Cenozoic. In Mali, its tests occur in abundance, especially at locality Mali-16, where the specimens typically had minimal preservational damage except for minor compression. At this location, all collected specimens were of nearly the same adult size, suggesting normal mortality and accumulation.

This taxon is regionally one of the most common echinoid species recovered, as it comes from four local sections in the Gao Trench and one in the Iullemmeden Basin; reports of it were first presented almost a century ago (Lambert and Perebaskine, 1930). In their review, Smith and Jeffery (2000) described this species as an early-late Paleocene taxon (with questionable Maastrichtian occurrences) that comes from several localities in Africa and the Arabian Peninsula. Those authors did not explicitly mention an occurrence in Mali, something that we confirm here and have previously reported (e.g., Claeson et al., 2010). We have recovered this species in the Paleocene rocks of all three major areas of our study: Taoudenit Basin, the Gao Trench and the Iullemmeden Basin. In each area it is found in limestones (Facies 3) suggesting relatively deep water. Prolific occurrence of this species

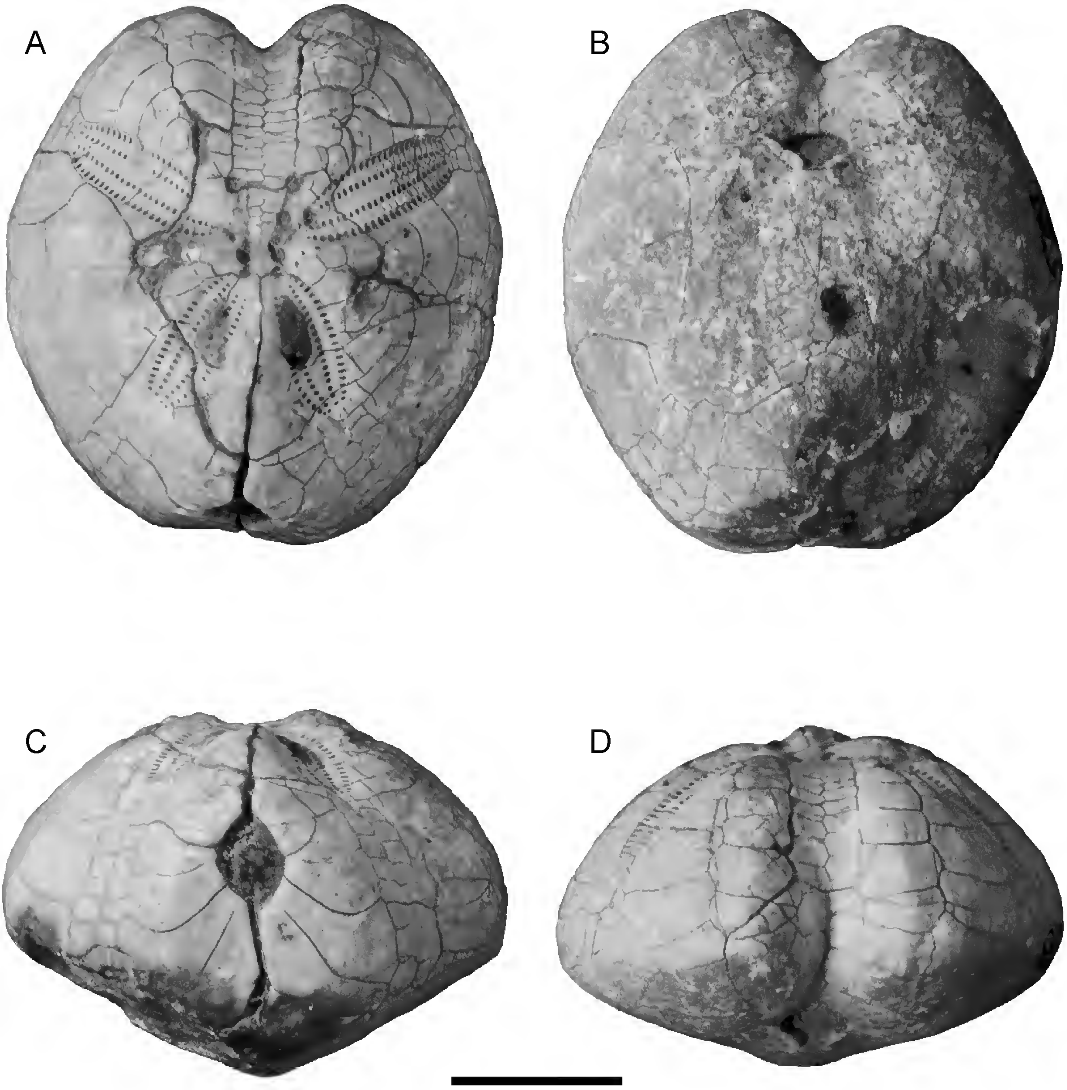


FIGURE 22. *Linthia sudanensis* (CNRST-SUNY 583), an echinoid from Mali-17 (unit 3), Paleocene of the Teberemt Formation, Gao Trench, in **A,** oral; **B,** aboral; **C,** posterior; and **D,** anterior views. Scale bar = 1 cm.

was used to establish the biogeographic framework for our correlated sections. A recent description of echinoderms at the K-Pg boundary did not list *Linthia,* or even Spatangoida as present in the internal regions of the Trans-Saharan seaway (Parma and Casadio, 2005: fig. 16), an omission that ignores the assignments of Smith and Jeffery (2000).

IRREGULARIA Latreille, 1825

NEOGNATHOSTOMATA Smith, 1981

PLESIOLAMPADIDAE Lambert, 1905

Oriolampas michelini Cotteau in Leymerie and Cotteau, 1856

Figures 23–25

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench, Taoudenit and Iullemmeden basins. Paleocene.

Localities: Mali-3/4 unit 3; Mali-7 unit 15; Mali-16 unit 2; Mali-17 units 2 and 3; Mali-18 units 1 and 3, and Mali-19 unit 1.

Depositional Environment: Limestone (Facies 3), open marine conditions.

Referred Material: CNRST-SUNY 74$^{7\text{ unit }15}$, 574–575$^{16\text{ units 1-2}}$; 601$^{17\text{ units 1-2}}$. Some specimens were identified in the field and not collected from every locality.

Description: Following Smith and Jeffrey (2000), Malian individuals of the irregular echinoid *Oriolampas michelini* have an ovate test with width 88%–92% of length. Test profile varies extensively from dome shaped to cone shaped. Malian specimens also show broad variation in absolute size (1.5–4 cm). Where visible, the peristome is oval to pentagonal in outline and recessed, and the periproct is slightly oval and subambital. Petals are of equal size and have a slight bowing to open distal end extending just short of the ambitus. Tuberculation is present on both oral and aboral sides on ambulacra and interambulacra. Where visible, the peristome is oval to pentagonal in outline and the periproct is slightly oval and subambital.

Discussion: Malian specimens are frequently preserved intact, with minor compression. Smith and Jeffery (2000) reported that *Oriolampas michelini* is a Late Paleocene species known from Europe and Africa, including Mali (i.e., the junior synonym, *Plesiolampas paquieri* Lambert and Perebaskine, 1930). Conical and more flattened specimens of *Oriolampas* are present in Malian localities, and it remains unknown what biological variables account for the fairly significant variance in profile. The presence of both forms of this taxon were used in the placement of Mali-7 in our correlated section. The species occurs in limestones (Facies 3) of open marine conditions. An infaunal organism, *Oriolampas* is generally well preserved and unlikely to have been transported far after death.

PHYMOSOMATOIDA Mortensen, 1904

STOMOPNEUSTOIDA Kroh and Smith, 2010

STOMECHINIDAE Pomel, 1883

Echinotiara perebaskinei Lambert, in Lambert and Perebaskine, 1930

Figure 26

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Localities: Mali-1 unit 4 and Mali-7 unit 11.

Depositional Environment: Limestone (Facies 3), open marine conditions; and shale (Facies 2), shallow, normal to restricted marine deposits.

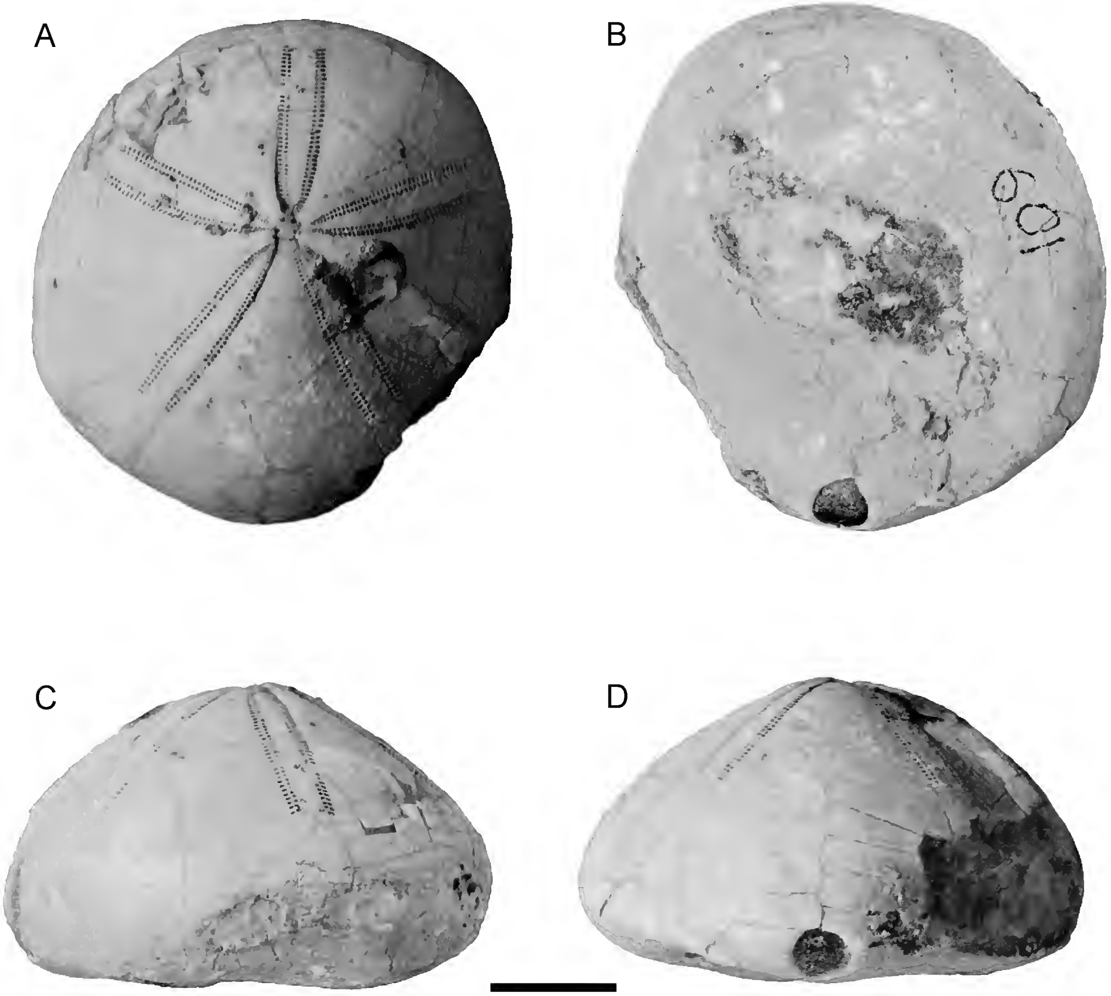


FIGURE 23. Taller morphotype of *Oriolampas michelini* (CNRST-SUNY 601), an echinoid from Mali-17 (units 1 and 2), Paleocene of the Teberemt Formation, Gao Trench, in **A,** oral; **B,** aboral; **C,** posterior; and **D,** anterior views. Scale bar = 1 cm.

Referred Material: CNRST-SUNY 179^{1}; 86, 103$^{7\text{-unit } 11}$.

Description: Diameter of test is ~30–35 mm at ambitus. Tests are round to slightly pentagonal. Apical disk is broken or obscured in Malian specimens; specimens have narrow ambulacral zones and broad interambulacral zones. Primary tubercles gradually diminish in size away from the ambitus. Trigeminate ambulacral plates have pore pairs that form arcs in groups of three.

Discussion: Smith and Jeffery (2000) reported that this regular echinoid is found only in the Maastrichtian and is distributed throughout Africa and the Arabian Peninsula, including the Gao region of Sudan (Lambert and Perebaskine, 1930). This taxon was used for biostratigraphy by helping to place both localities from which it was collected. It was found both in the Iullemmeden and Taoudenit basins but not in the Gao Trench (figs. 1D and plate 1). In general, regular urchins occur as epibenthic grazers in open marine condi-

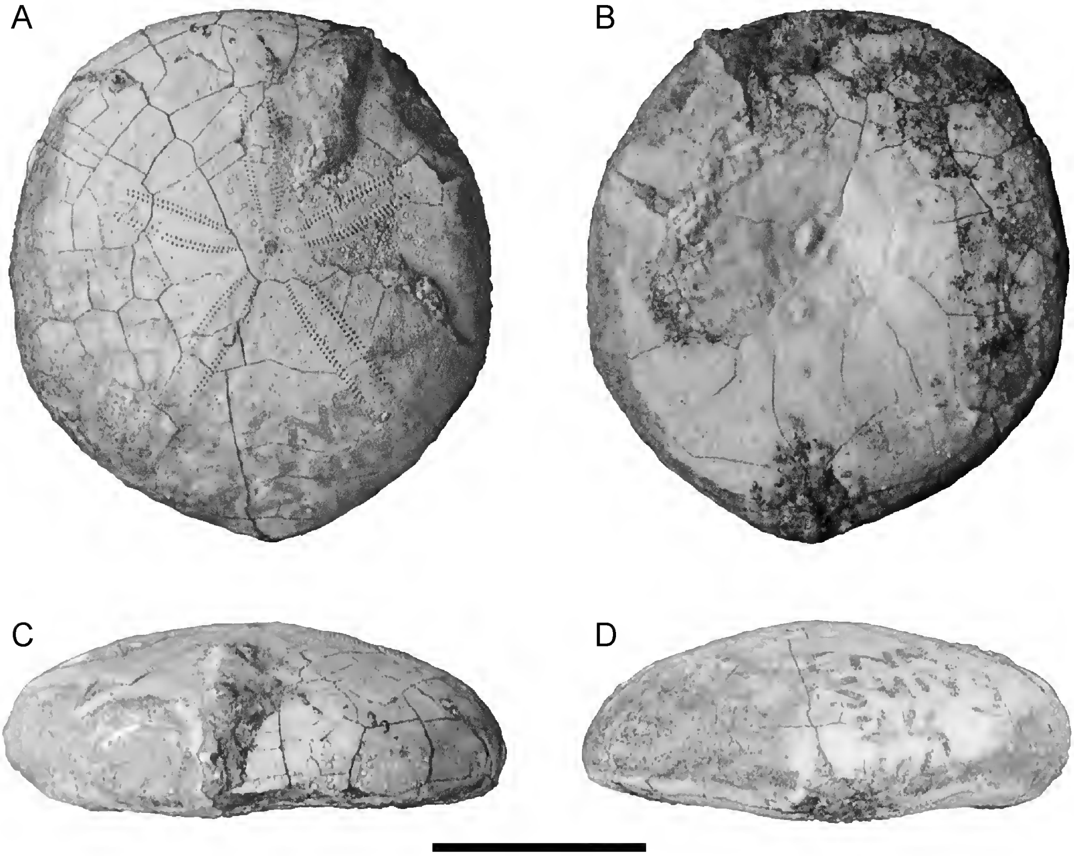


FIGURE 24. Flatter morphotype of *Oriolampas michelini* (CNRST-SUNY 74), an echinoid from Mali-7 (unit 15), early Paleocene, lower Teberemt Formation, Iullemmeden Basin in **A,** oral; **B,** aboral; **C,** posterior; and **D,** anterior views. Scale bar = 1 cm.

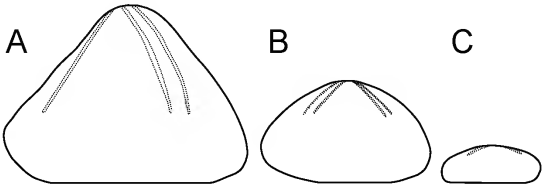


FIGURE 25. Lateral outlines of three fossil echinoids from the Paleocene of the Teberemt Formation, showing variability in size and shape within the species *Oriolampas michelini*. **A,** CNRST SUNY 575 (Mali-16 units 1 and 2); **B,** CNRST-SUNY 601 (Mali-17 units 1 and 2); and **C,** CNRST-SUNY 74 (Mali-7 unit 15). A and B from the Gao Trench, C from the Iullemmeden Basin. Scale bar = 1 cm.

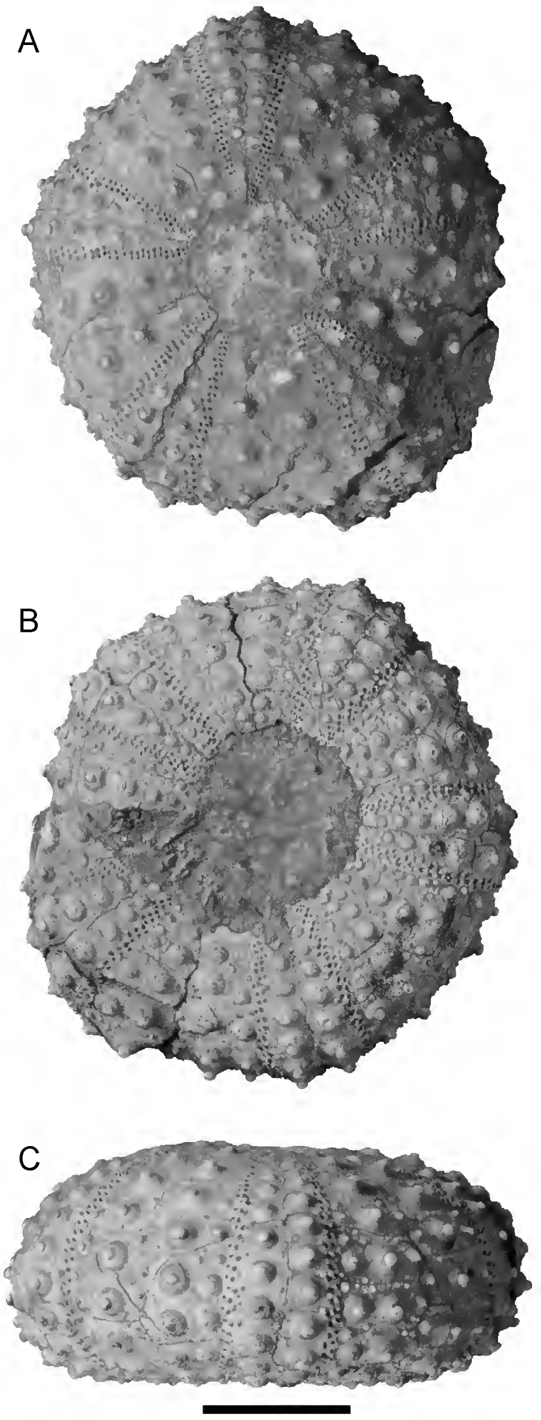


FIGURE 26. *Echinotiara perebaskinei* (CNRST-SUNY 86), an echinoid from Mali-7 (unit 11), Paleocene, lower Teberemt Formation, Iullemmeden Basin in **A**, oral; **B**, aboral; and **C**, posterior views. Scale bar = 1 cm.

tions from nearshore to littoral settings. Specific habitat or community associations are as yet unknown for this species.

MOLLUSCA Linnaeus, 1758

CEPHALOPODA Cuvier, 1795

NAUTILOIDEA Agassiz, 1847

Nautiloidea indet.

Figure 27

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded marl and shale (Facies 4), shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 473.

Description: Partially complete cast of shell with the simple suture pattern of Nautiloidea.

NAUTILIDA Agassiz, 1847

HERCOGLOSSIDAE Spath, 1927

Deltoidonautilus Spath, 1927

?*Deltoidonautilus* sp.

Figure 28

Horizon in Study Area and Age: Teberemt Formation of the Iullemmeden Basin. Paleocene.

Locality: Mali-11 unit 2.

Depositional Environment: Alternating shales and limestones, Facies 2, indicating shallow, normal-to-restricted marine lagoons and open platform settings and Facies 3, indicating small-patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 471.

Description: Cast is lenticular with angular, bluntly V-shaped venter. Umbilicus covered with matrix, limiting identification.

Discussion: Specimen is similar to those figured by (Adegoke, 1977). *Deltoidonautilus* has a

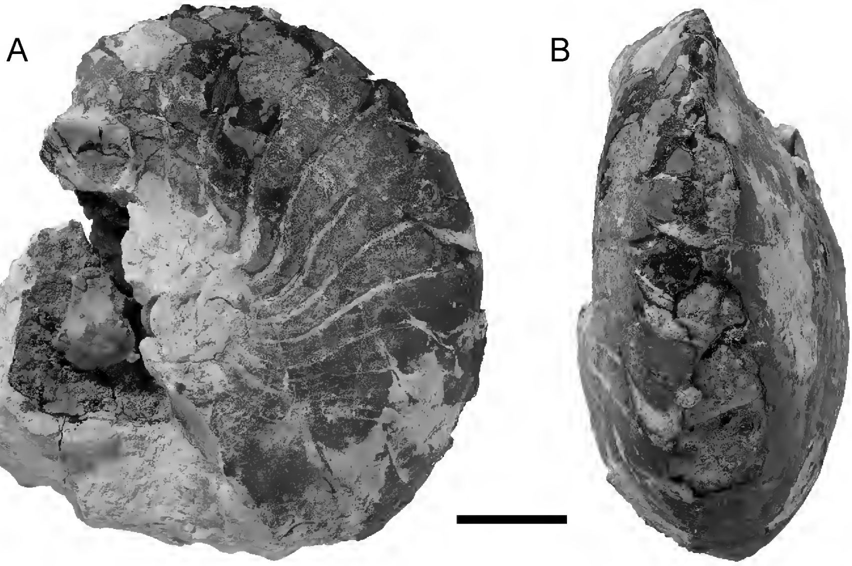


FIGURE 27. Casts (formed in situ) of Nautiloidea indet. (CNRST-SUNY 473), a cephalopod from Mali-17 (unit 3), Paleocene of the Teberemt Formation, Gao Trench in **A,** left lateral and **B,** ventral views. Scale bar = 2 cm.

stratigraphic range from the Upper Cretaceous to the Oligocene (Kummel et al., 1964).

Cimomia reymenti Adegoke, 1977

Figure 29

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-7 unit 13.

Depositional Environment: Limestone (Facies 3); oysters in patch reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 474.

Description: Infilled cast with height-to-width ratio of approximately two to one; has gentle flexed septa and the final chamber appears more than half a whorl long, although preservation limits confirmation.

Discussion: Species first described by Adegoke (1977). *Cimomia* ranged from Late Cretaceous to Oligocene and had a global distribution (summarized in Casadío et al., 1999).

Cimomia ogbei Adegoke, 1977

Figures 30, 31

Horizons in Study Area and Age: Teberemt Formation of the Gao Trench, Tamaguélelt Formation of the Taoudenit Basin. Paleocene-Eocene.

Localities: Mali-18 unit 8 and Mali-21 (unit unspecified).

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 475$^{18\text{-unit 8}}$ and 476^{21}.

Description: Infilled casts. Venter is broadly rounded, shell has a subspherical shape, height to width ratio is one to one, septa are thick and gently sinuous. Species is distinguished by many septate shells and its extremely broad venter.

?*Cimomia* sp.

Figure 32

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

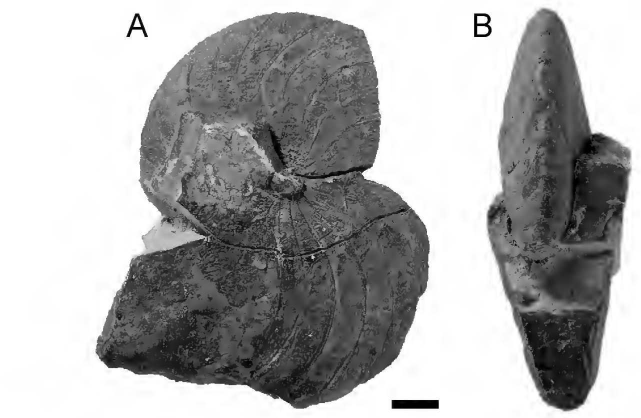


FIGURE 28. Casts (formed in situ) of Cephalopoda from Mali 11 (unit 2), Paleocene of the Teberemt Formation, Iullemmeden Basin, Mali: ?*Deltoidonautilus* sp. (CNRST-SUNY 471) in **A,** left lateral and **B,** apertural views from the Paleocene of the Teberemt Formation. Scale bar = 1 cm.

Locality: Mali 16 unit 1.

Depositional Environment: Interbedded marl and shale (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 472.

Description: Very poorly preserved, infilled cast of shell that is reminiscent of *Cimomia*.

AMMONITIDA Hyatt, 1889

SPHENODISCIDAE Hyatt, 1900

Libycoceras crossense Zaborski, 1982

Figure 33A, B

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-8 unit 12.

Depositional Environment: Limestones (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 19.

Description: Partial cast preserving suture patterns figured in Claeson et al. (2010: fig. 2). Discoidal, involute shell with sharp venter and faint ribs. Suture pattern is similar to that previously described for this species (Zaborski and Morris, 1999).

Discussion: *Libycoceras* has a stratigraphic range from Upper Campanian through Upper Maastrichtian, as does the species *L. crossense* (Zaborski and Morris, 1999). Reyment (1980) argued that the shallow depth of the Trans-Saharan Seaway, as well as the likely fluctuations in salinity, made it an atypical environment for ammonites, however, sphenodiscids are common in nearshore facies (Ifrim and Stinnesbeck, 2010). Reyment (1980) noted that Niger has Trans-Saharan Seaway deposits of numerous ammonites that he interpreted as mass die-offs, but we have not observed this phenomenon in Malian sediments.

Libycoceras Zaborski, 1982

Libycoceras sp.

Figure 33C–E

Horizon in Study Area and Age: Probably Ménaka Formation of the Iullemmeden and Taoudenit basins. Maastrichtian.

Localities: Mali-1 and Mali-7.

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 129^{7}; 176^{1}.

Description: CNRST-SUNY 129 was not recovered in situ but most likely comes from Maastrichtian deposits. Discoidal, involute shell with sharp venter and faint ribs. Suture pattern is not well preserved enough to determine species.

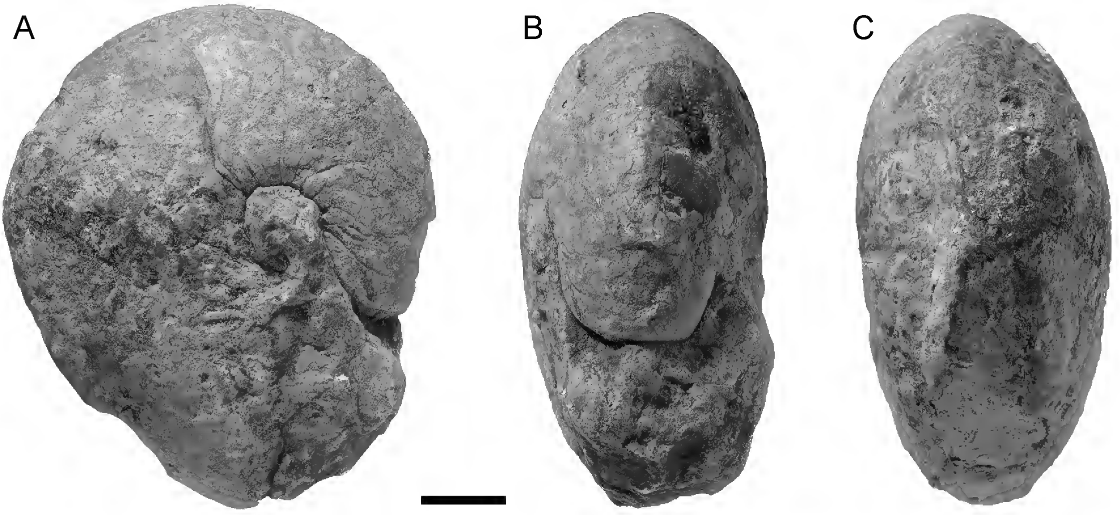


FIGURE 29. Casts (formed in situ) of Cephalopoda from the Maastrichtian limestones of the Ménaka Formation, Iullemmeden Basin: *Cimomia reymenti* (CNRST-SUNY 474) in **A,** right lateral; **B,** apertural; and **C,** ventral views. Scale bar = 2 cm.

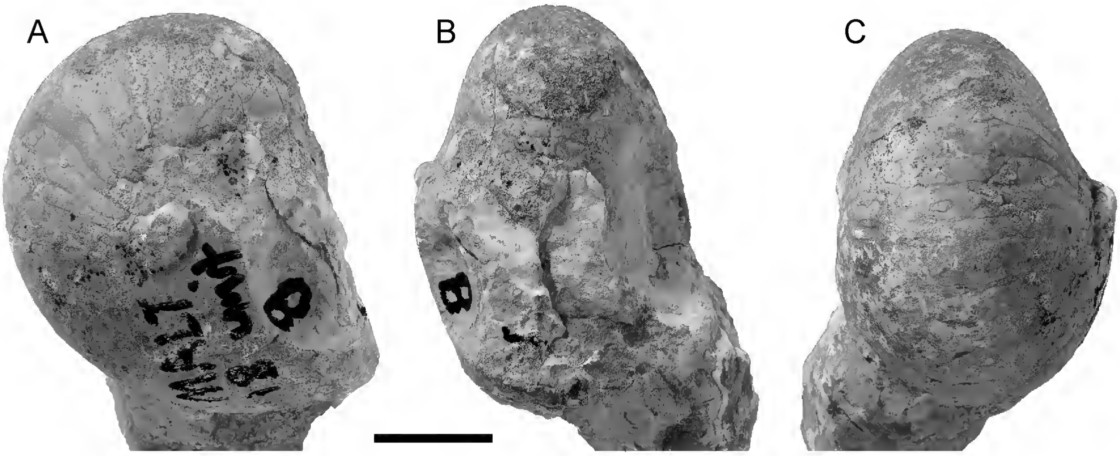


FIGURE 30. Casts (formed in situ) of Cephalopoda from the Paleocene of the Teberemt Formation, Gao Trench. *Cimomia ogbei* (CNRST-SUNY 475) in **A,** right lateral; **B,** apertural; and **C,** ventral views. Matrix is cropped at bottom of photo. Scale bar = 2 cm.

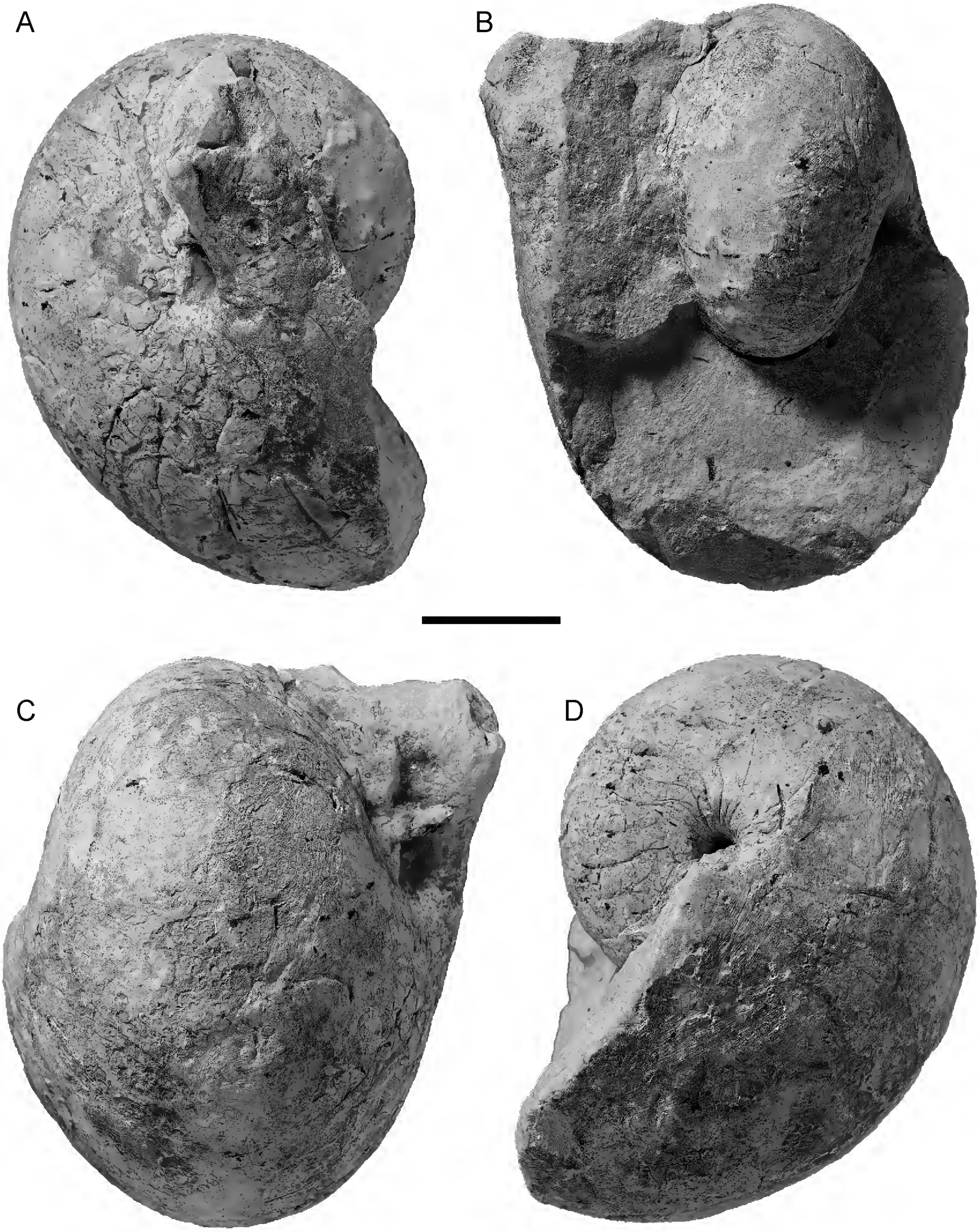


FIGURE 31. Cephalopoda, *Cimomia ogbei* (CNRST-SUNY 476) cast (formed in situ) from the Eocene of the Tamaguélelt Formation, Taoudenit Basin in **A,** right lateral; **B,** apertural; **C,** ventral; and **D,** left lateral views. Note the extensive matrix infill visible in B. Scale bar = 2 cm.

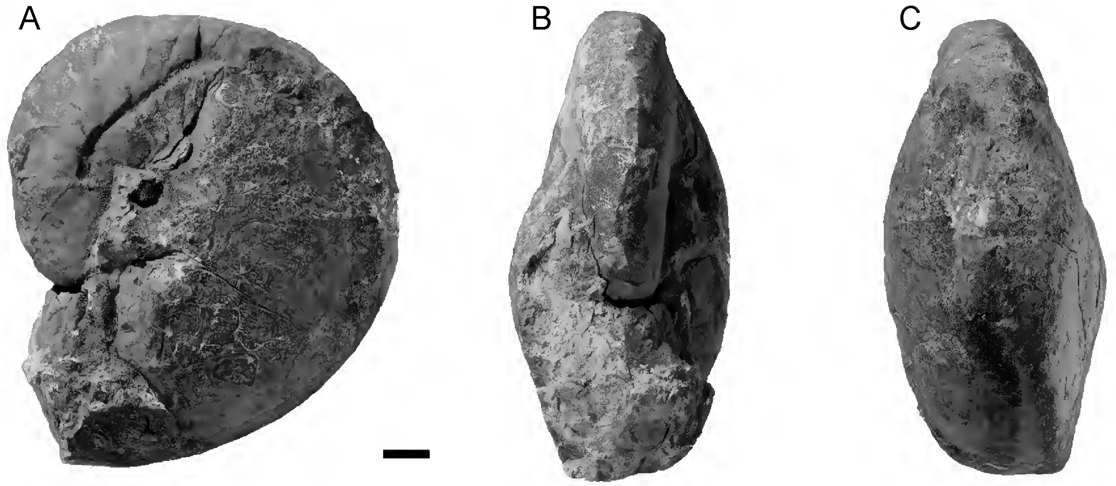


FIGURE 32. Casts (formed in situ) of Cephalopoda from the Paleocene of the Teberemt Formation, Gao Trench. ?*Cimomia* sp. (CNRST-SUNY 472) in **A,** left lateral; **B,** apertural; and **C,** ventral views. Scale bar = 2 cm.

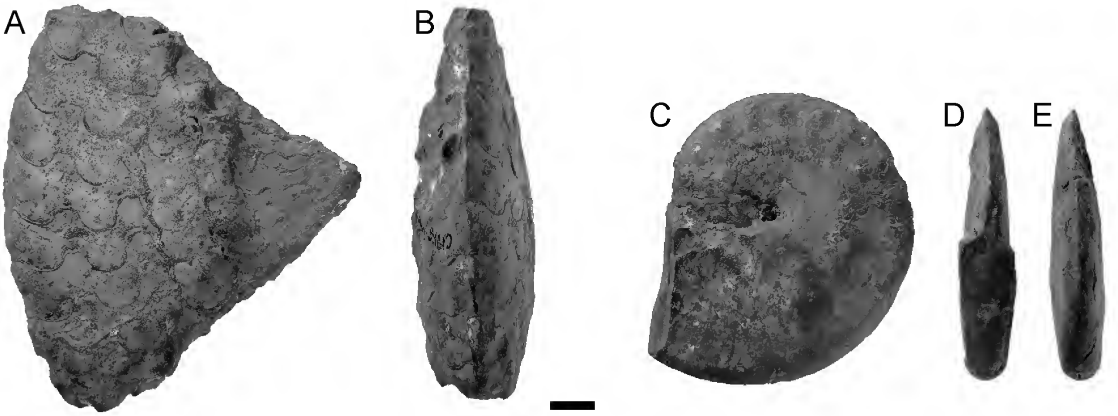


FIGURE 33. Casts (formed in situ) of *Libycoceras crossense* (CNRST-SUNY 19) from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali in **A,** right lateral; and **B,** ventral views; and *Libycoceras* sp. (CNRST-SUNY 129), probably also from the Ménaka Formation but not collected in situ, in **C,** left lateral; **D,** apertural; and **E,** ventral views. Same scale bar = 1 cm for A and B and 2 cm for C–E.

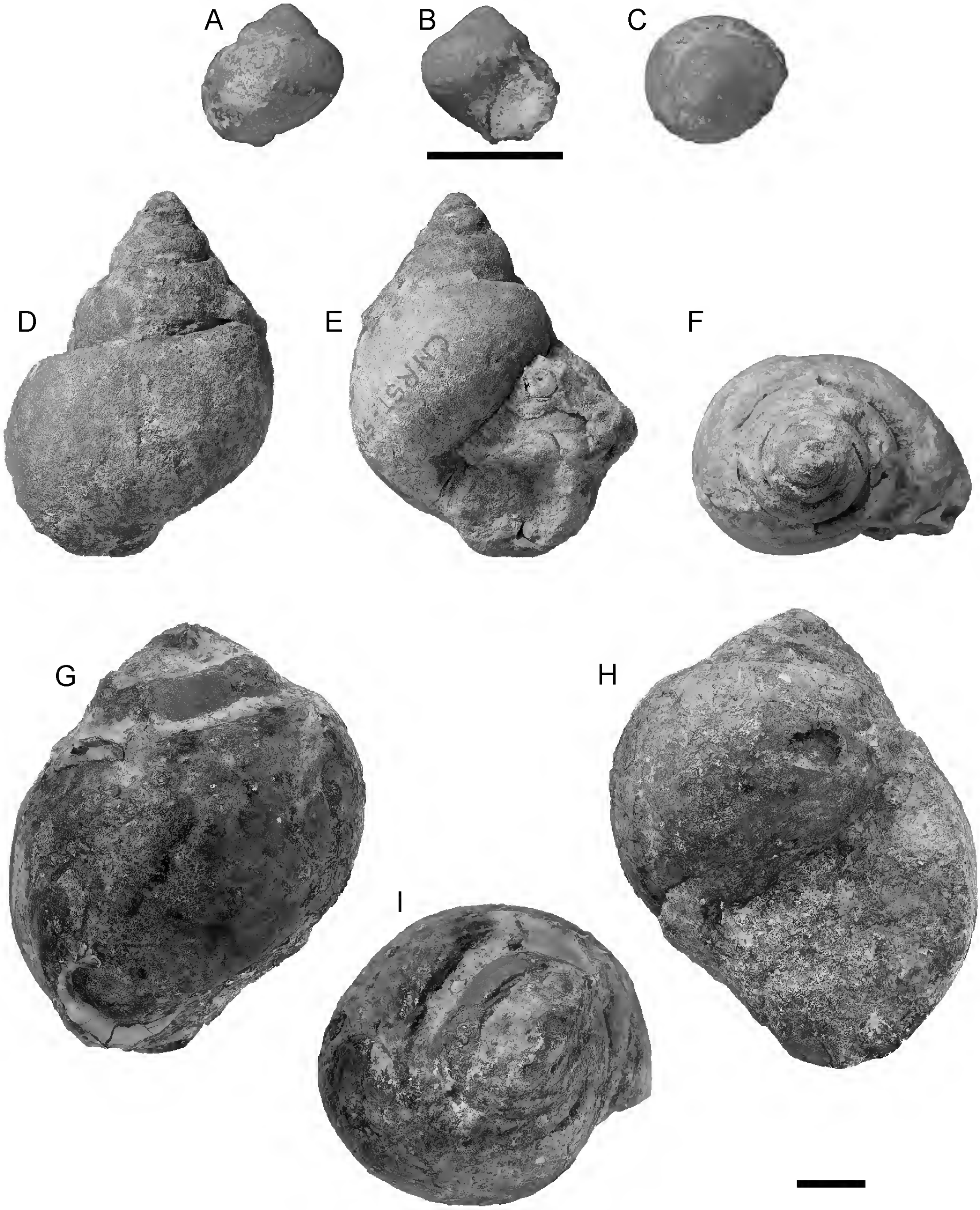


FIGURE 34. Casts (formed in situ) of Gastropoda from the Cretaceous-Paleogene boundary of the Ménaka Formation, Taoudenit Basin, Mali. ?*Euspira* (CNRST-SUNY 177d) in **A,** abapertural; **B,** apertural; and **C,** apical views; and from the Paleocene Teberemt Formation, *Crommium nigeriense* (CNRST-SUNY159) in **D,** abapertural; **E,** apertural; and **F,** apical views; and ?*Polinices* sp. (CNRST-SUNY 484) in **G,** abapertural; **H,** apertural; and **I,** apical views. A–C share a scale bar separate from that of and D–I. Both scale bars = 1 cm.

GASTROPODA Cuvier, 1795

SORBEOCONCHA Ponder and Lindberg, 1977

CAMPANILOIDEA Douvillé, 1904

AMPULLINIDAE Cossman and Peyrot, 1919

Crommium nigeriense Adegoke, 1977

Figure 34D–F

Horizon in Study Area and Age: Teberemt Formation of the Taoudenit Basin. Paleocene.

Locality: Mali-3, probably unit 3.

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 159.

Description: Conical cast with prominently elevated spire of approximately five whorls; body whorl large and inflated. Aperture appears hemispherical; umbilicus obscured by matrix.

CERITHIOIDEA Fleming, 1822

?Cerithioidea indet.

Figure 35

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench, Taoudenit and Iullemmeden basins. Paleocene.

Localities: Mali-1, probably top of unit 4; Mali-11, probably unit 2; Mali-17 unit 3.

Depositional Environment: Mali-1, limestone (Facies 3), indicating small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity; Mali-17, interbedded marl and shale (Facies 4), indicating shallow, sublittoral open marine settings with water depths <50 m; Mali-11, alternating shale and marl: Facies 2, indicating shallow, normal-to-restricted marine lagoons and open platform settings and Facies 3 (see above).

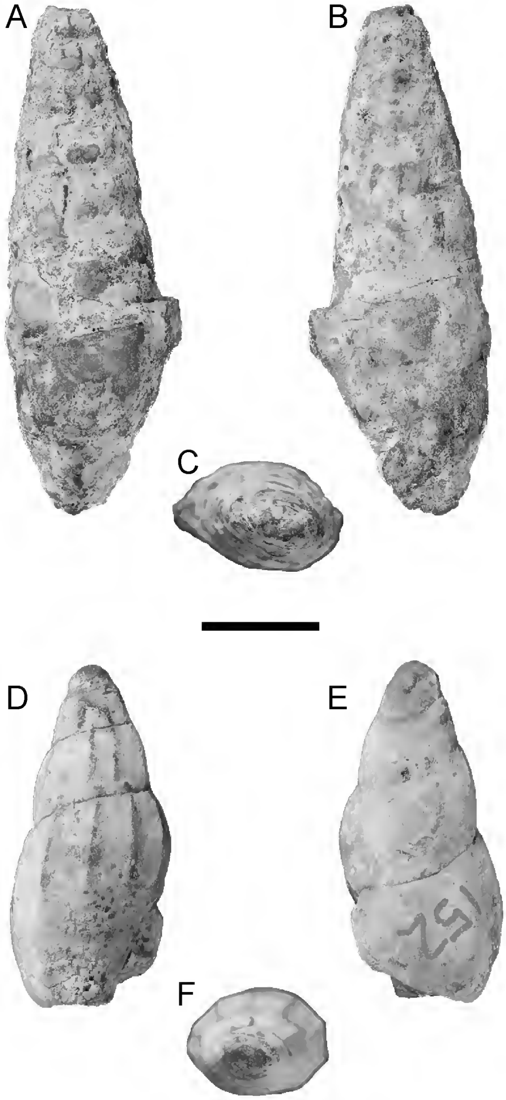


FIGURE 35. Casts (formed in situ) of Gastropoda from the Paleocene of the Teberemt Formation: ?Cerithioidea indet. (CNRST-SUNY 541) in **A,** apertural; **B,** abapertural; and **C,** apical views, from the Paleocene/Eocene Boundary of the Teberemt Formation, Gao Trench; and ?Cerithioidea indet. (CNRST-SUNY 152) from similar deposits but in the Iullemmeden Basin in **D,** apertural; **E,** abapertural; and **F,** apical views. Scale bar = 1 cm.

Referred Material: CNRST-SUNY 152[11], and 541–542[17-unit 3].

Description: Terebriform shell with high spire; siphonal notch broken or obscured.

Discussion: Cerithioidea are most common in tropical and subtropical waters and inhabit marine, brackish, and freshwater environments.

TURRITELLIDAE Lovén, 1847

Haustator Montfort, 1810

"*Haustator*" sp.

Figure 36 A–F

Horizon in Study Area and Age: Teberemt Formation of the Iullemmeden Basin. Paleocene.

Locality: Mali-11, probably unit 2.

Depositional Environment: Alternating shale and marl: Facies 2; shallow, normal-to-restricted marine lagoons and open platform settings and Facies 3; small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 63a–c.

Description: Partial casts of small-sized, carinate turritellids with a deep suture and whorls that increase gently in diameter as added. Apices and apertures missing.

Discussion: The systematics of turritellids are poorly understood, and most families and genera are "inadequately defined and poorly studied," according to Waite and Allmon (2016: 247); see also Allmon (2011). Thus, identifications of these taxa are considered tentative and a variety of forms are illustrated to highlight the diversity of this group within the Mali sediments.

TURRITELLINAE Lovén, 1847

Turritellinae indet. "A"

Figure 36G–L

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-18, probably unit 2.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 489a–c.

Description: Partial casts of turritellines with pronounced primary and secondary ribs and faint suture. Aperture missing in specimens shown in figure 37C–F, and partially obscured by matrix in figure 37A, B. Apices missing in all. The whorl profile of Turritellinae indet. "A" differs from the subquadrate profile of Turritellinae indet. "B" and the convex whorl profile of Turritellinae indet. "C"; Turritellinae indet. "A" has prominent primary and secondary ribs, whereas Turritellinae indet. "B" and Turritellinae indet. "C" do not.

Discussion: Turritellinae are common inhabitants of shallow coastal settings in Cretaceous through modern oceans (Allmon, 2011). We note that this specimen, which is a cast of a shell, comes from a phosphatic conglomerate that tends not to preserve calcitic body fossils (Tapanila et al., 2008).

Turritellinae indet. "B"

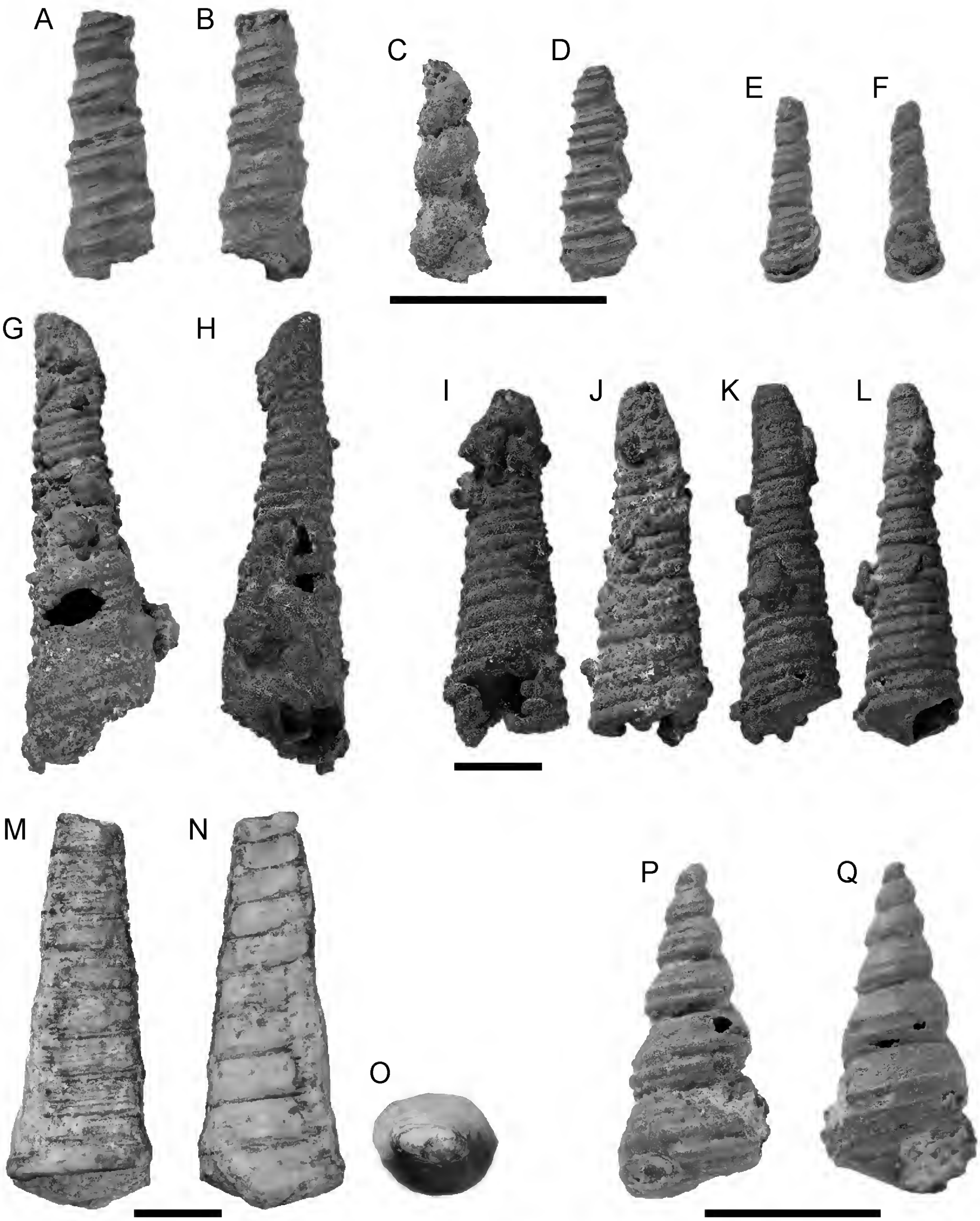
Figure 36M–O

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 2.

FIGURE 36. Casts (formed in situ) of Gastropoda from the Paleocene-Eocene boundary of the Teberemt Formation. "*Haustator*" sp., CNRST-SUNY 63a, in **A,** apertural and **B,** abapertural views; CNRST-SUNY 63b in **C,** apertural and **D,** abapertural views; and CNRST-SUNY 63c in **E,** abapertural and **F,** apertural views; three specimens of Turritellinae indet. "A": CNRST-SUNY 489a, in **G,** abapertural and **H,** apertural views; CNRST-SUNY 489b in **I,** apertural and **J,** abapertural views; and CNRST-SUNY 489c in **K,** abapertural and **L,** apertural views; Turritellinae indet. "B" (CNRST-SUNY 490) in **M,** abapertural; **N,** apertural; and **O,** apical views; ?*Mesalia* sp. (CNRST-SUNY 63d) in **P,** abapertural and **Q,** apertural views. A–F and P–Q Iullemmeden Basin localities, and G–O, Gao Trench localities. Scale bars: A–L = 1 cm; M–Q = 5 mm.

→


A
B
C
D
E
F
G
H
I
J
K
L
M
N
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P
Q

Depositional Environment: Shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 490.

Description: Partial cast of a turritelline with subquadrate whorl profile, faint spiral ribs and at least 10 whorls. Aperture and apex missing. See Turritellinae indet. "A" above for characteristics distinguishing different forms.

Turritellinae indet. "C"

Figure 9

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-7 unit 12.

Depositional Environment: Alternating limestone and shale: Facies 2, indicating shallow, normal-to-restricted marine lagoons and open platform settings and Facies 3, indicating small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 114.

Description: Molds and casts of turritellines with a convex whorl profile, spiral ribs, and whorls that increase moderately in diameter as added. See Turritellinae indet. "A" above for characteristics distinguishing different forms.

Discussion: CT scanning of the limestone specimen (AMNH Microscopy and Imaging Facility; GE Phoenix V|tome|x s 240 system; scan parameters 220 kV and 96 microns/voxel; rotational projections reconstructed with Datos X software and Volume Graphics Studio Max 2.2) yielded a 3D-image that displayed density differences between the rock and empty cavities resulting from shells having dissolved following deposition and lithification. This finding led to the recognition of molds and casts of turritelline gastropods throughout the rock fragment, not just on the visible outer edges. While most of the molds were empty, some contained secondary calcite crystals. 23 such fossils were highlighted in the scan (others are likely present but were not pursued at this time). Because most of these shell indicators are completely intact and include apices, which are frequently broken in fossils, we infer that this assemblage was buried quickly. Above, in the description of the Ménaka Formation, we noted that in these sediments these high-spired gastropods were subparallel and pointed in a N-S orientation.

Mesalia Gray, 1847

?*Mesalia* sp.

Figure 36P, Q

Horizon in Study Area and Age: Teberemt Formation of the Iullemmeden Basin. Paleocene.

Locality: Mali-11.

Depositional Environment: Probably unit 2, interbedded limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity and shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 63d.

Description: Partial cast of a turritellid with whorls that inflate as they are added, as is common in *Mesalia*; aperture partially obscured by matrix. Prominent primary and secondary ribs, sutural area indented.

NATICOIDEA Guilding, 1834

NATICIDAE Guilding, 1834

Euspira Agassiz, 1837

?*Euspira* sp.

Figure 34A–C

Horizon in Study Area and Age: Teberemt Formation of the Taoudenit Basin Paleocene.

Locality: Mali-1.

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm

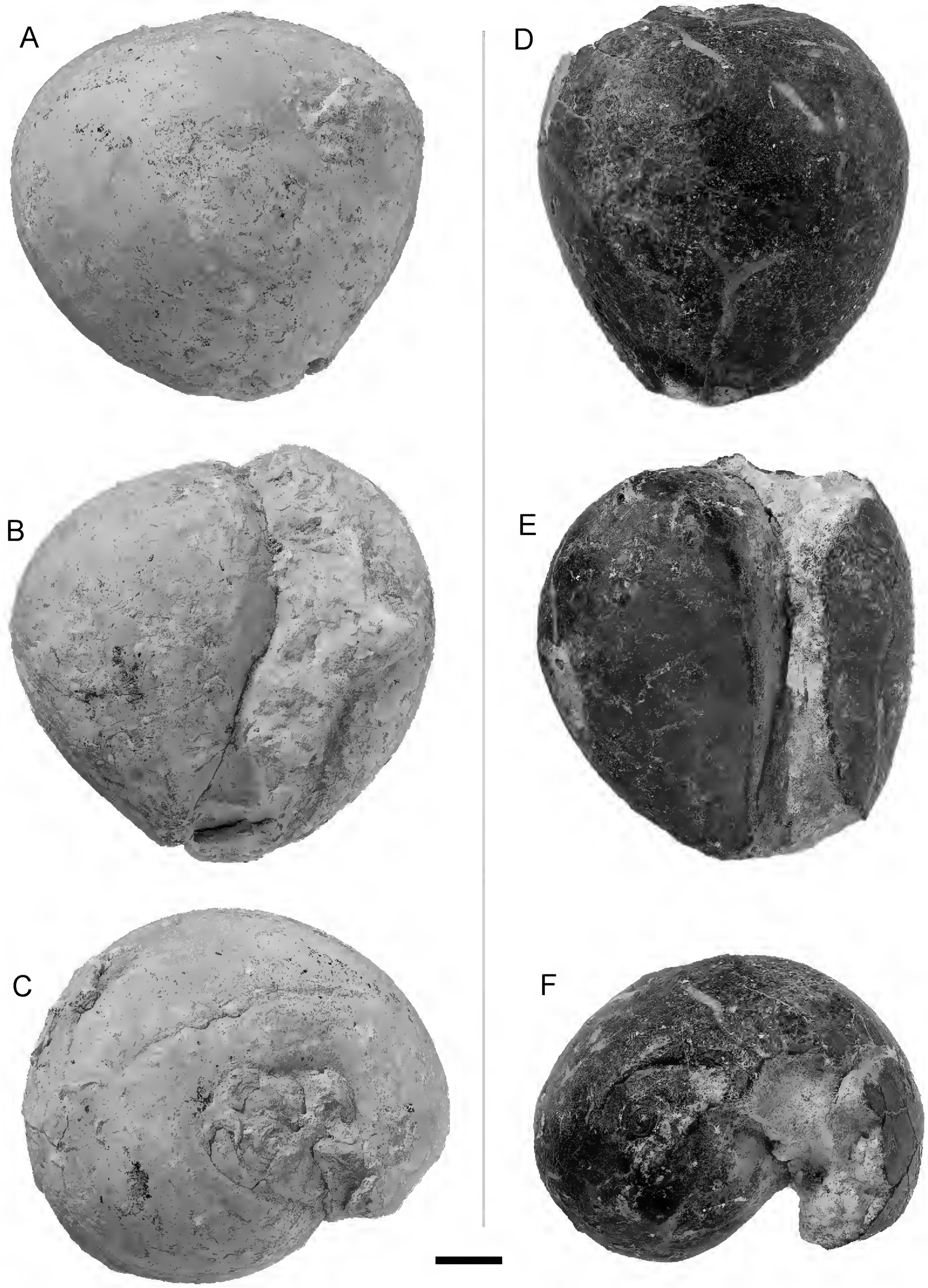


FIGURE 37. Casts (formed in situ) of Gastropoda Eocypraeidae indet. from the Paleocene of the Teberemt Formation, Gao Trench. CNRST-SUNY 485 in **A,** abapertural; **B,** apertural; and **C,** apical views; and CNRST-SUNY 486 in **D,** abapertural; **E,** apertural; and **F,** apical views. Scale bar = 1 cm.

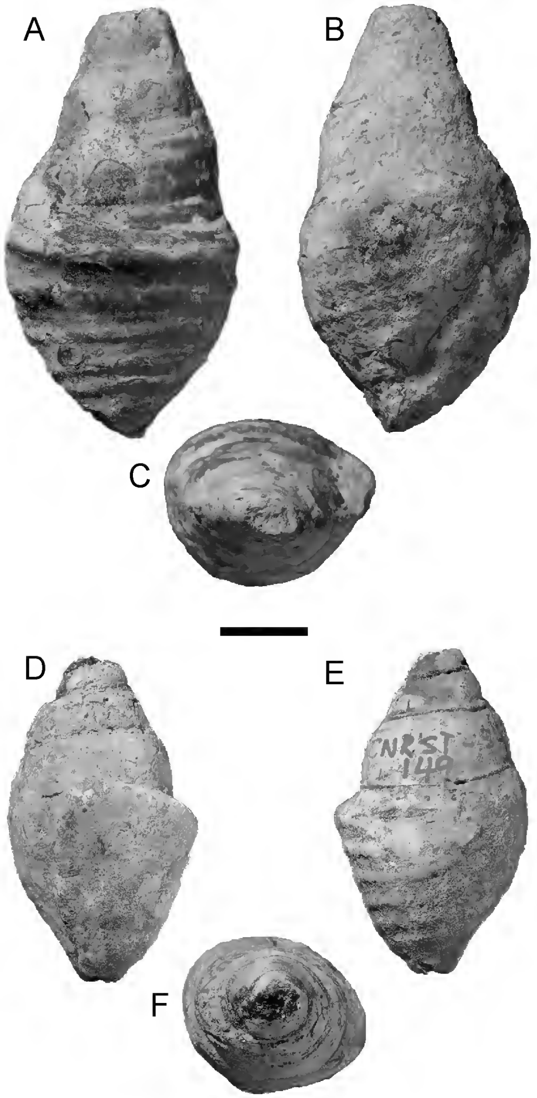


FIGURE 38. Casts (formed in situ) of Gastropoda: from the Cretaceous-Paleogene boundary of the Teberemt Formation, Gao Trench. ?Stromboidea indet. (CNRST-SUNY 483) in **A,** abapertural; **B,** apertural; and **C,** apical views; and from the Paleocene of the Teberemt Formation, Iullemmeden Basin: ?Stromboidea indet. (CNRST-SUNY 149) in **D,** apertural; **E,** abapertural; and **F,** apical views. Scale bar = 1 cm.

beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 177d.

Description: Small globose shell with about three whorls, an inflated body whorl and a semilunar aperture.

Polinices Montfort, 1810

?*Polinices* sp.

Figure 34G–I

Horizon in Study Area and Age: Teberemt Formation of the Iullemmeden Basin. Paleocene.

Locality: Mali-11, probably unit 2.

Depositional Environment: Interbedded limestones and paper shales. Facies 2, indicating shallow, normal-to-restricted marine lagoons and open platform settings and Facies 3, indicating small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 484.

Description: Poorly preserved cast of a naticid gastropod with a short spire of about three low whorls, body whorl large and inflated. Aperture and umbilicus are obscured by matrix.

LATROGASTROPODA Riedel, 2000

CYPRAEOIDEA Rafinesque, 1815

EOCYPRAEIDAE Schilder, 1924

Eocypraeidae indet.

Figure 37

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 485 and CNRST SUNY 486.

Description: These casts are ovate and subglobose, narrow anteriorly, and have poorly preserved apertures, making fine-scale identification difficult.

Discussion: Adegoke (1977) and Newton et al. (1922) figured several genera and species within Eocypraeidae from late Paleocene to early Eocene deposits of Nigeria. The Eocypraeidae is composed primarily of extinct taxa; the Cypraeoidea superfamily has a tropical to subtropical distribution in modern oceans.

STROMBOIDEA Rafinesque, 1815

?Stromboidea indet.

Figure 38

Horizons in Study Area and Age: Teberemt Formation of the Iullemmeden Basin and the Gao Trench. Cretaceous-Paleocene.

Localities: Mali-1, most likely unit 2; Mali-17 unit 3.

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity, which is in places interbedded with shale (Facies 2), indicating shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 141, 142, 149[11] and 483[17].

Description: Poorly preserved conical casts with high spire, prominent spiral ribs, and possible shoulder. Apex missing and aperture obscured by matrix.

ROSTELLARIIDAE Gabb, 1868

Tibia Röding, 1798

Tibia sp.

Figure 39A–C

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

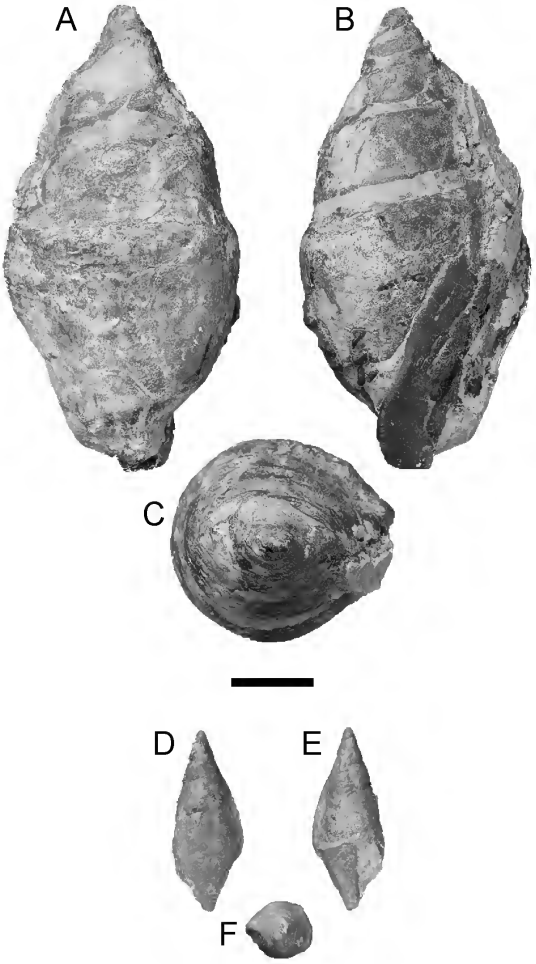


FIGURE 39. Casts (formed in situ) of Gastropoda, taxa from the Paleocene of the Teberemt Formation. *Tibia* sp. (CNRST-SUNY 480) from the Gao Trench in **A,** abapertural; **B,** apertural; and **C,** apical views; and ?*Calyptraphorus* sp. (CNRST-SUNY 177a) from the Taoudenit Basin in **D,** abapertural; **E,** apertural; and **F,** apical views. Scale bar = 1 cm.

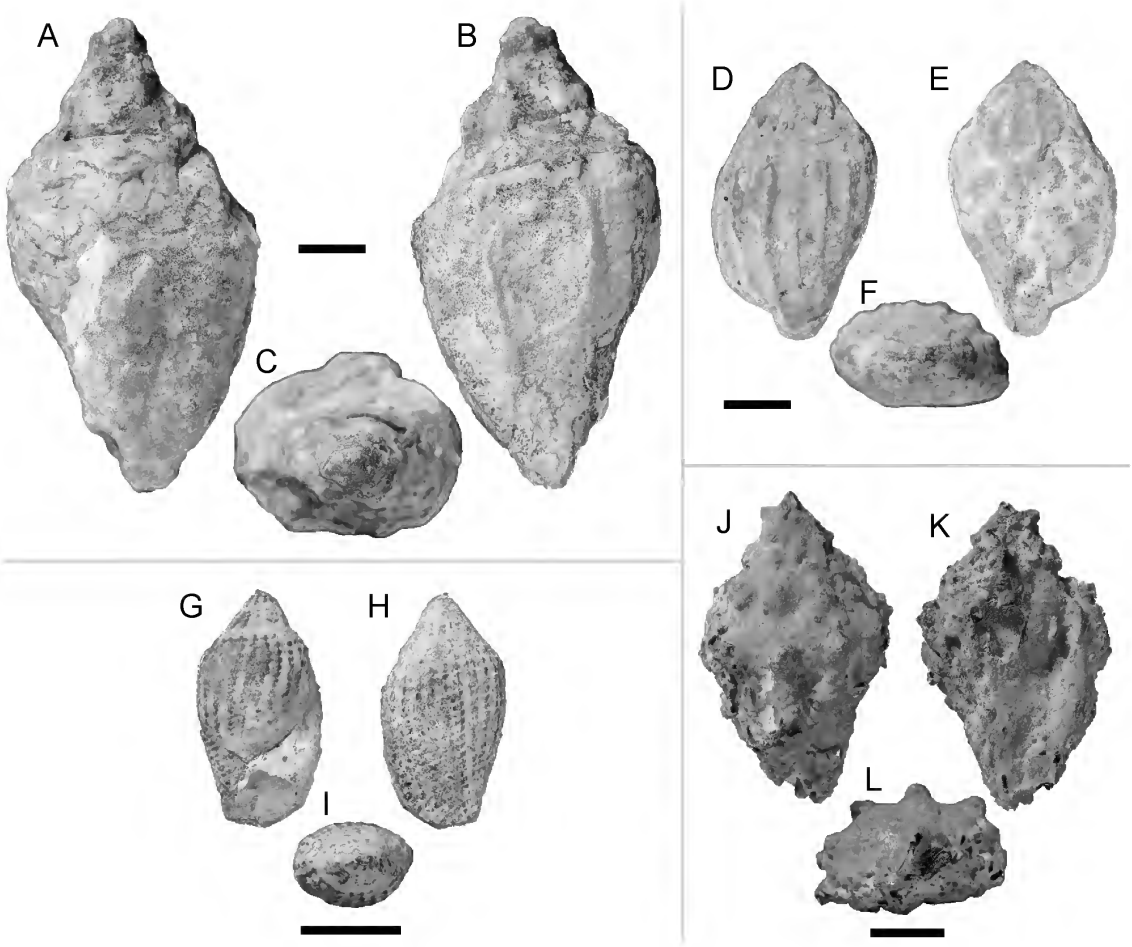


FIGURE 40. Casts (formed in situ) of Gastropoda from the Paleocene of the Teberemt Formation, Gao Trench. ?*Volutilithes* sp. (CNRST-SUNY 509) in **A,** apertural; **B,** abapertural, and **C,** apical views; ?*Athleta* sp. "A" (CNRST-SUNY 508) in **D,** abapertural; **E,** apertural; and **F,** apical views; ?*Athleta* sp. "B" (CNRST-SUNY 496) in **G,** apertural; **H,** abapertural; and **I,** apical views. ?*Cornulina* sp. (CNRST-SUNY 518) in **J,** abapertural; **K,** apertural; and **L,** apical views. Scale bars: A–F = 1 cm; G–L = 5 mm. Note the compression and distortion in F and I.

Depositional Environment: Alternating limestone and shale: Facies 2; shallow, normal-to-restricted marine lagoons and open platform settings and Facies 3; small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 480 and 481.

Description: Two casts recovered have the characteristic strong lip and deep suture of this genus.

Discussion: Specimens are similar to *Rostellaria* of (Newton et al., 1922: pl. 3: 3-9), species of which have been subsumed within other strombid genera such as *Tibia* and *Rimella* (e.g., Squires, 2013). Strombidae has a tropical to subtropical distribution in modern oceans.

Calyptraphorus Conrad, 1858 ("1857")

?*Calyptraphorus* sp.

Figure 39D–F

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-1.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 177a.

Description: Cast with fusiform outline and polished surface due to callus cover.

Discussion: Specimens are similar to the Paleocene *Rimella ewekoroensis* of Nigeria (Adegoke, 1977), which is not *Rimella* but likely *Calyptraphorus* (Squires, 2013).

NEOGASTROPODA Wenz, 1938

VOLUTOIDEA Rafinesque, 1815

VOLUTIDAE Rafinesque, 1815

Volutilithes Swainson, 1840

?*Volutilithes* sp.

Figure 40A–C

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded marl and shale (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 509–510.

Description: Poorly preserved high-spired conical casts with faintly visible axial costae. Aperture obscured by matrix.

Athleta Conrad, 1853a

?*Athleta* sp. "A"

Figure 40D–F

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 507–508.

Description: Short-spired cast with medium-spaced axial costae; infilled aperture limits identification.

Discussion: Volutidae are found throughout most of the world's oceans, from littoral to abyssal depths (Darragh and Ponder, 1998). Differs from ?*Athleta* sp. "B" in the spacing of the axial costae.

?*Athleta* sp. "B"

Figure 40G–I

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 units 2 and 3.

Depositional Environment: Interbedded shale and marl (Facies 4) interpreted as shallow, sublittoral open marine settings with water depths <50 m and shale (Facies 2) interpreted as shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 496, 532.

Description: Short-spired cast with prominent closely spaced axial costae and striae; infilled aperture limits identification.

Discussion: Differs from ?*Athleta* sp. "A" in the spacing of the axial costae.

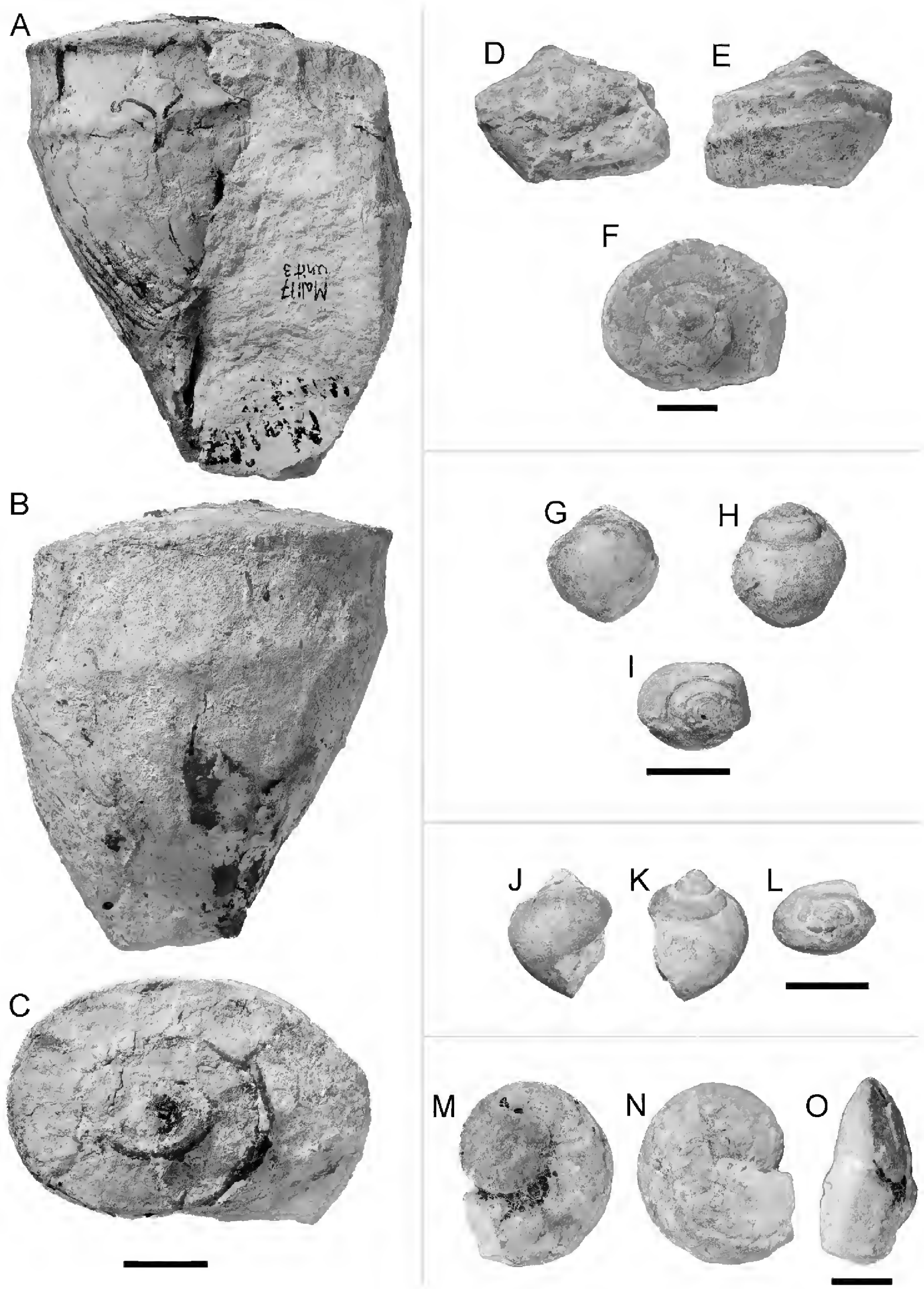


FIGURE 41. Casts (formed in situ) of Gastropoda. From the Paleocene of the Teberemt Formation, Gao Trench: two specimens of *Heligmotoma* ?*oluwolei*: CNRST-SUNY 492 in **A,** apertural; **B,** abapertural; and **C,** apical views; and CNRST-SUNY 533 in **D,** apertural; **E,** abapertural; and **F,** apical views; ?*Pseudoliva* sp., CNRST-SUNY 495a in **G,** apertural; **H,** abapertural; and **I,** apical views; and CNRST-SUNY 495b in **J,** apertural; **K,** abapertural; and **L,** apical views. From the Eocene of the Tamaguélelt Formation, Taoudenit Basin, Trochoidea indet. (CNRST-SUNY 540) in **M,** apical; **N,** umbilical; and **O,** apertural views. Note extensive matrix infill in A, and the compression and distortion in C, I, L, and O. Scale bars: A–C = 2 mm; D–L = 1 cm; M–O = 5 mm.

BUCCINOIDEA Rafinesque, 1815

MELONGENIDAE Gill, 1871

Cornulina Conrad, 1853b

?*Cornulina* sp.

Figure 40J–L

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 518.

Description: Spire whorls with strong nodes that are not in exact rows. Cast is distorted and covered in matrix, limiting identification.

Heligmotoma ?*oluwolei* Adegoke, 1977

Figure 41A–F

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 492, 533.

Description: Large cast, spire only slightly elevated above apical surface; large body whorl that encompass the entire cast. Appears to have the diagnostic features of a noded shoulder keel and apical groove.

Discussion: Species first described by Adegoke (1977).

Pseudoliva Swainson, 1840

?*Pseudoliva* sp.

Figure 41G–L

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 494a-b; 495a-b.

Description: Poorly preserved small globose shell cast with a short spire and about 4 whorls, with an inflated body whorl. Aperture obscured by matrix. Figure 41I and 41L show evidence of compression and distortion in both referred specimens.

VETIGASTROPODA Salvini-Plawen, 1980

TROCHOIDEA Rafinesque, 1815

Trochoidea indet.

Figure 41M–O

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Tamaguélelt Formation of the Taoudenit Basin. Paleocene-Eocene.

Locality: Mali 17 unit 3; Mali-21.

Depositional Environment: Interbedded marl and shale (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 506[17] and 540[21].

Description: Very poorly preserved trochiform cast, short spired, umbilicus and aperture obscured by matrix.

BIVALVIA Linnaeus, 1758

OSTREIDA Férussac, 1822

Ostreida indet.

Figures 42, 43, 44

Horizons in Study Area and Age: Ménaka and Teberemt formations of the Iullemmeden Basin; Teberemt Formation of the Gao Trench, and Teberemt and Tamaguélelt formations of the Taoudenit Basin. Maastrichtian-Eocene.

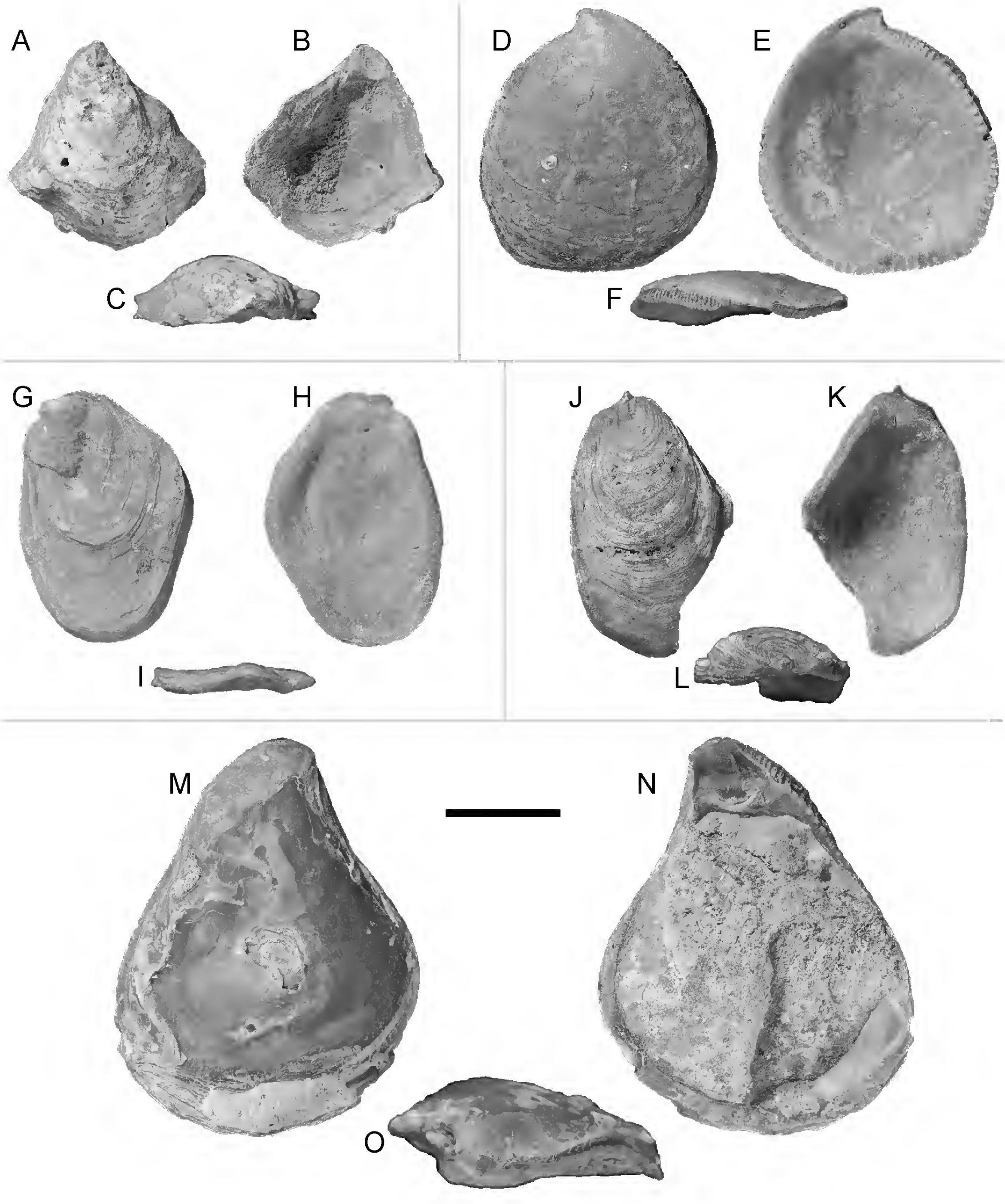


FIGURE 42. Shells of Bivalvia. Ostreida indet., from the Paleocene of the Teberemt Formation, Gao Trench: CNRST-SUNY 498a, in **A,** right valve exterior; **B,** right valve interior; and **C,** right valve dorsal views; CNRST-SUNY 498d in **D,** left valve exterior; **E,** left valve interior; and **F,** left valve dorsal views; CNRST-SUNY 498b, in **G,** left valve exterior; **H,** left valve interior; and **I,** left valve dorsal views, and CNRST-SUNY 498c in **J,** right valve exterior; **K,** right valve interior; and **L,** right valve dorsal views. Ostreida indet. from the Eocene of the Tamaguélelt Formation Taoudenit Basin, CNRST-SUNY 501, in **M,** right valve exterior; **N,** right valve interior; and **O,** right valve dorsal views. Scale bar = 1 cm.

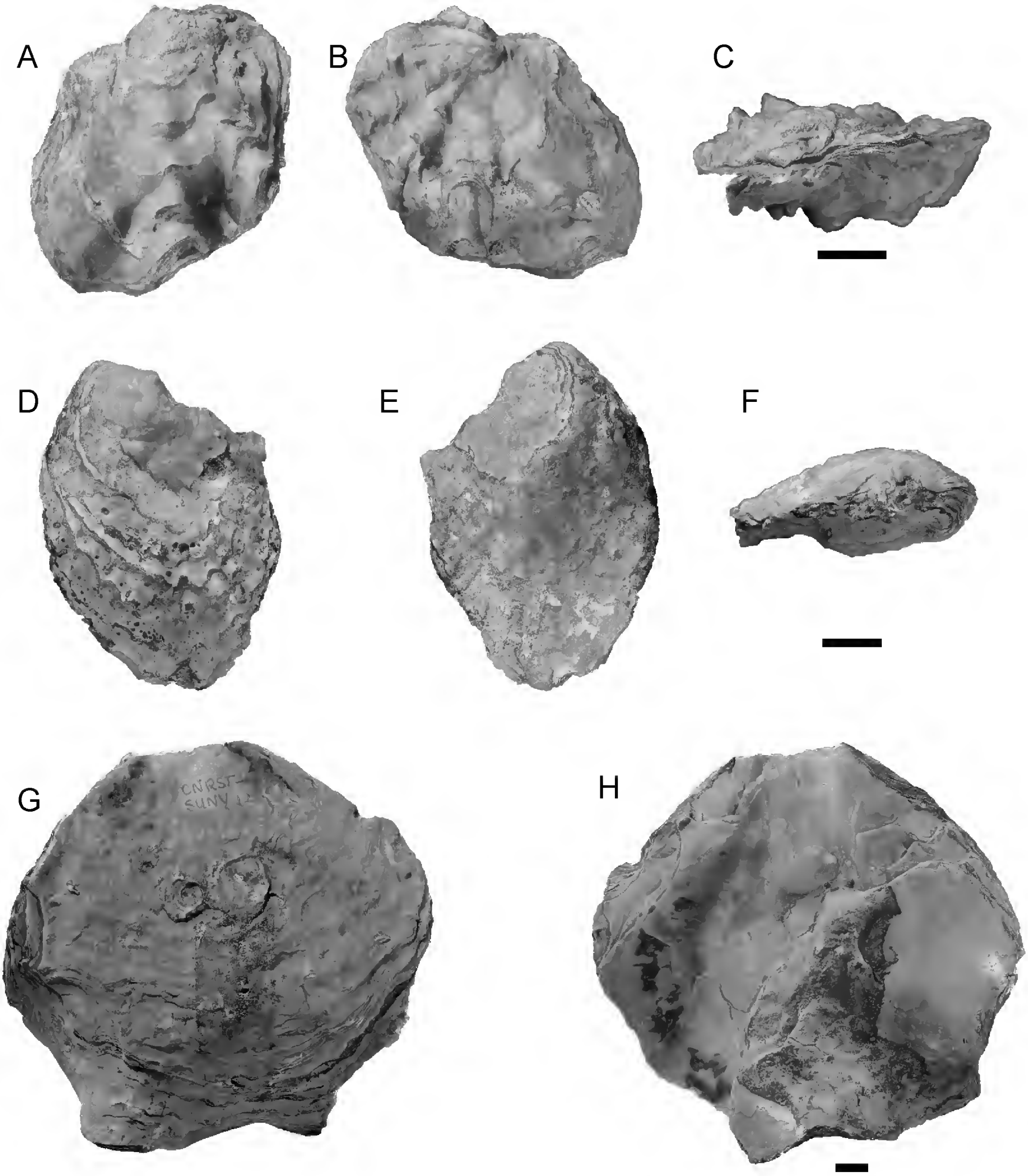


FIGURE 43. Articulated shells of Bivalvia, Ostreida indet. CNRST-SUNY 84 from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin in **A,** left valve; **B,** right valve; and **C** dorsal views; CNRST-SUNY 554 from the Paleocene Teberemt Formation, Gao Trench in **D,** right valve; **E,** left valve and **F,** dorsal views; and CNRST-SUNY 128 from the Paleocene/Eocene boundary of the Teberemt Formation, Iullemmeden Basin in **G,** right valve exterior and **H,** right valve interior views. Scale bars = 1 cm.

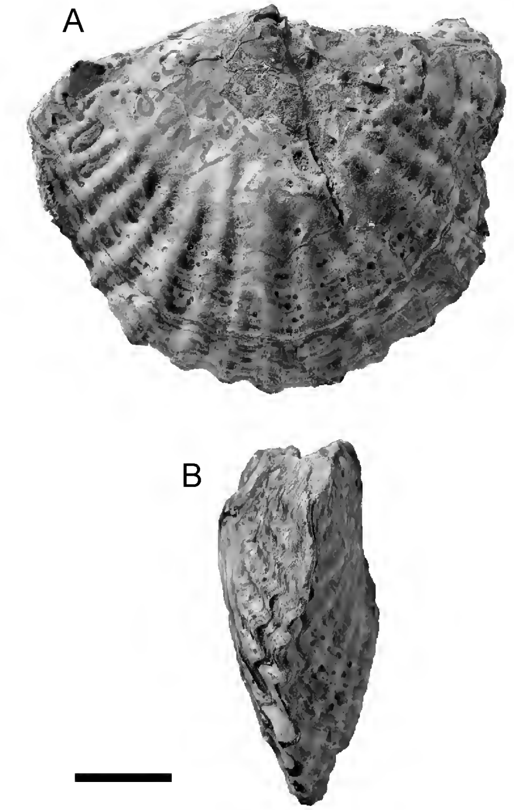


FIGURE 44. Ostreida indet. from the Paleocene/Eocene Boundary of the Teberemt Formation, Iullemmeden Basin, Mali. CNRST-SUNY 145 in **A,** right valve and **B,** posterior views. Shells appear to be chemically altered. Scale bar = 1 cm.

Localities: Mali-7 unit 11; Mali-10/11 unit 2; Mali-17 unit 2; Mali-18 probably unit 2; Mali-21, most likely one of the carbonate-rich units.

Depositional Environment: Shale, marl and shale, and limestone (facies 2–4) interpreted as ranging from small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity, to shallow, normal-to-restricted marine lagoons and open platform settings, and shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY $84^{7\text{-unit }11}$, $105^{7\text{-unit }11}$, $128^{10\text{-unit }2}$, $145–146^{11\text{-unit }2}$, $554^{17\text{-unit }2}$, 498a–$d^{18\text{-unit }2}$; 501^{21}, 561^{21}.

Description: Large shells, some that appear to be chemically altered, and casts that are inequivalve and inequilateral, many displaying foliated layers and irregular quadrate shapes.

Discussion: Fossil ostreids are common constituents of the Malian fauna in most fossiliferous areas of our section, especially in the Cretaceous portion. Ostreida shells are known to be highly plastic and therefore difficult to identify (e.g., Stanley, 1970). A variety of forms are illustrated to highlight the diversity of this group within the Mali sediments. The family Ostreidae are the so-called true oysters and there are several other oysterlike groups within the order Ostreida. Based on current evidence, the Mali specimens cannot be classified with more precision than we provide. Members of Ostreida are common inhabitants of shallow coastal settings, particularly tropical and temperate seas, in Cretaceous through modern oceans (Mikkelsen and Bieler, 2008). As noted above the taphonomy at locality Mali-17 in the Teberemt Formation of the Gao Trench is such that a turtle skeleton acted as a functional substrate for an ostreid colony.

OSTREOIDEA Rafinesque, 1815

OSTREIDAE Rafinesque, 1815

Ostreidae indet.

Figure 45

Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin and either the Teberemt or Tamaguélelt formations of the Taoudenit Basin. Maastrichtian and Paleogene.

Localities: Mali-7 unit 11 and Mali-21.

Depositional Environment: Shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 90, 99, 101.

Description: CNRST-SUNY 101 is a disarticulated left valve with strongly crenulated margins. Figure 45 shows the adductor muscle scar and chomatal pits around nearly the entire margin.

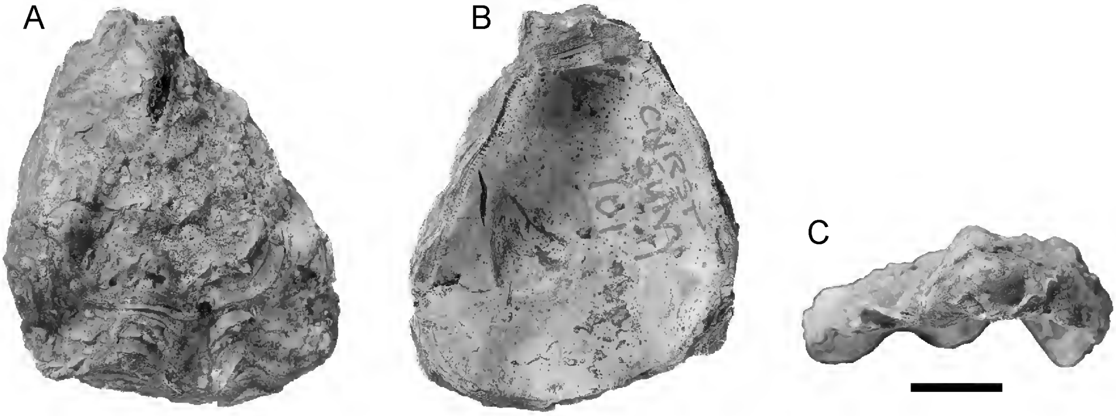


FIGURE 45. Shell of Bivalvia from the Maastrichtian Ménaka Formation, Iullemmeden Basin, Mali. Ostreidae indet. (CNRST-SUNY 101) in **A,** left valve exterior; **B,** left valve interior; and **C,** left valve dorsal views. Shell appears to be chemically altered. Scale bar = 1 cm.

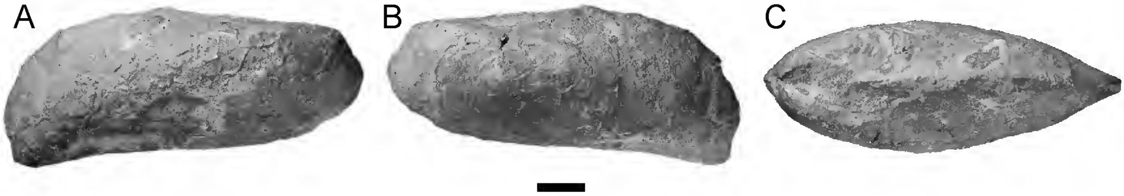


FIGURE 46. Cast (formed in situ) of Bivalvia from the Paleocene of the Teberemt Formation, Gao Trench. ?Arcidae indet. (CNRST-SUNY 547) in **A,** right valve; **B,** left valve; and **C,** dorsal views. Cast formed with valves articulated. Scale bar = 1 cm.

ARCIDA Stoliczka, 1871

ARCOIDEA Lamarck, 1809

?Arcidae Lamarck, 1809

Arcidae indet.

Figure 46

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded shale and marl (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 547.

Description: Articulated elongate and quadrate cast, with a straight hinge and what appears to be a wide ligament.

Discussion: In the modern ocean, the Arcidae are most common in intertidal to shallow settings; some species can tolerate estuarine and fresh waters (Mikkelsen and Bieler, 2008).

GLYCYMERIDIDAE Dall, 1908

Trigonarca Conrad, 1862

Trigonarca sp.

Figure 47

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-7 unit 11.

Depositional Environment: Shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

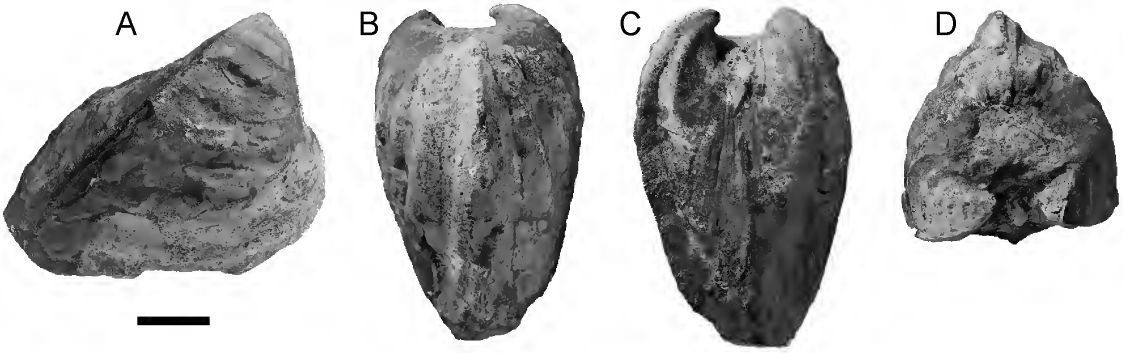


FIGURE 47. Cast (formed in situ) of articulated Bivalvia from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin. *Trigonarca* sp. (CNRST-SUNY 85) in **A,** right valve; **B,** posterior; **C,** anterior; and **D,** dorsal views. Scale bar = 1 cm.

Referred Material: CNRST-SUNY 78, 85, 98.

Description: Cast with subtrigonal shape, broad hinge plate, strong subhorizontal to commarginal costae imprints.

Discussion: The bivalve genus *Trigonarca* is known only from the Cretaceous (Newell, 1969), and its presence at Mali-7 unit 11 constrains the placement of the Cretaceous-Paleogene boundary at this locality and in the composite section.

PECTINIDA Gray, 1854

PLICATULOIDEA Gray, 1854

PLICATULIDAE Gray, 1854

Plicatula Lamarck, 1801

?*Plicatula* sp.

Figure 48

Horizon in Study Area and Age: Teberemt Formation of the Iullemmeden Basin and the Gao Trench. Paleocene.

Localities: Mali-11, probably unit 2; Mali-17 unit 3; Mali-19.

Depositional Environment: Alternating shale and limestone; Facies 2: shallow, normal-to-restricted marine lagoons and open platform settings, and Facies 3: small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 148^{11}, 535$^{17\text{-unit }3}$, and 551^{19}

Description: Strong and wide ribbing, and ventrally rounded fan shape is suggestive of *Plicatula.*

PALAEOHETERODONTA Newell, 1965

UNIONIDA Stoliczka, 1871

UNIONIDAE Rafinesque, 1820

?Unionidae indet.

Figure 49

Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin and Teberemt Formation of the Gao Trench. Maastrichtian-Paleocene.

Localities: Mali-7 unit 12; Mali-17 unit 3.

Depositional Environment: Interbedded marl and shale (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 122$^{7\text{-unit }12}$ and 497$^{17\text{-unit }3}$.

Description: Articulated rhomboidal inflated casts with strong concentric growth rings that form ridges, and prominent posterior ridge extending from the beak that is suggestive of Unionidae. Because specimen is articulated, diagnostic features, such as the hinge teeth, are not visible.

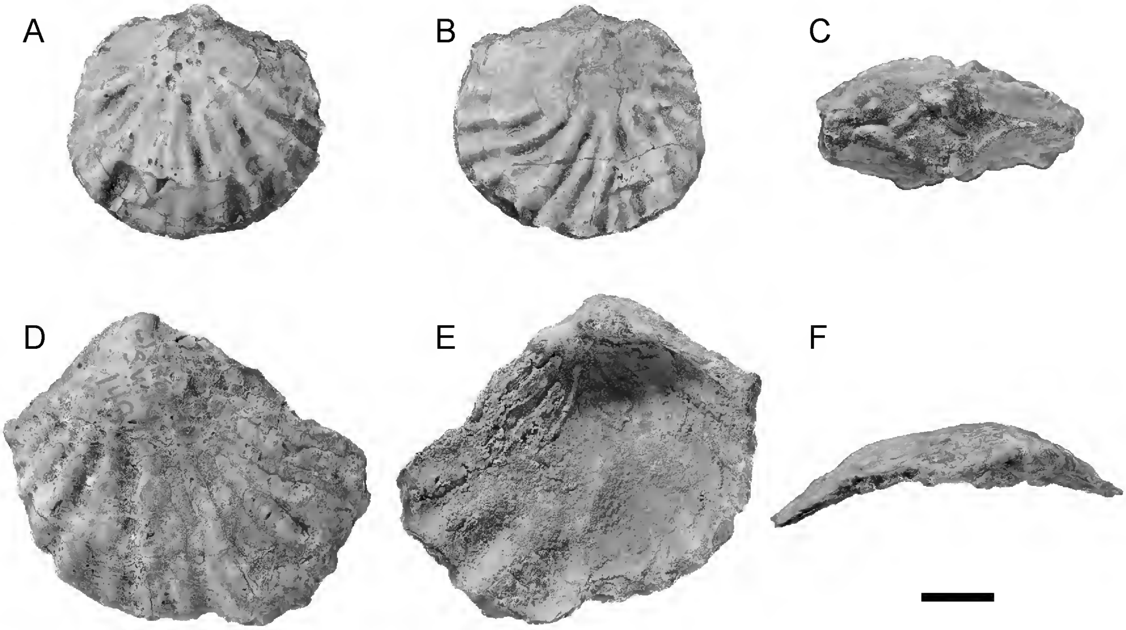


FIGURE 48. Shells of Bivalvia. Articulated ?*Plicatula* sp., CNRST-SUNY 535, from the Paleocene of the Teberemt Formation of the Gao Trench in **A,** right valve; **B,** left valve; and **C,** dorsal views; a disarticulated valve of ?*Plicatula* sp. (CNRST-SUNY 148) from the Paleocene/Eocene boundary of the Teberemt Formation of the Iullemmeden Basin, Mali in **D,** right valve exterior; **E,** right valve interior; and **F,** right valve dorsal views. Shells appear to be chemically altered. Scale bar = 1 cm.

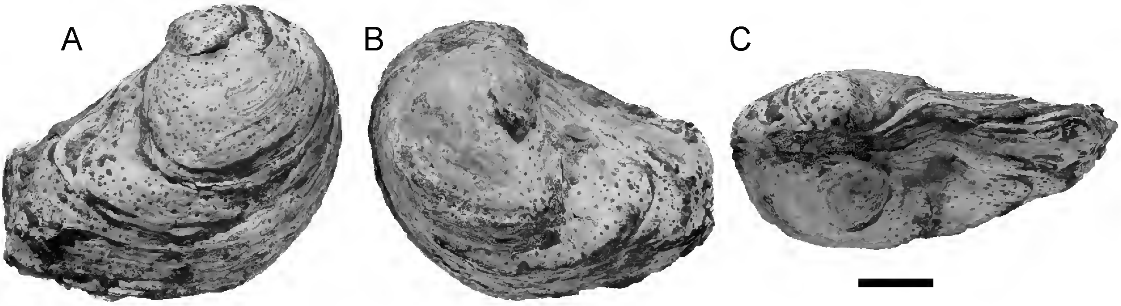


FIGURE 49. Shell of articulated Bivalvia from the Paleocene of the Teberemt Formation of the Gao Trench. ?Unionidae indet. (CNRST-SUNY 497) in **A,** left valve; **B,** right valve; and **C,** dorsal views; Scale bar = 1 cm.

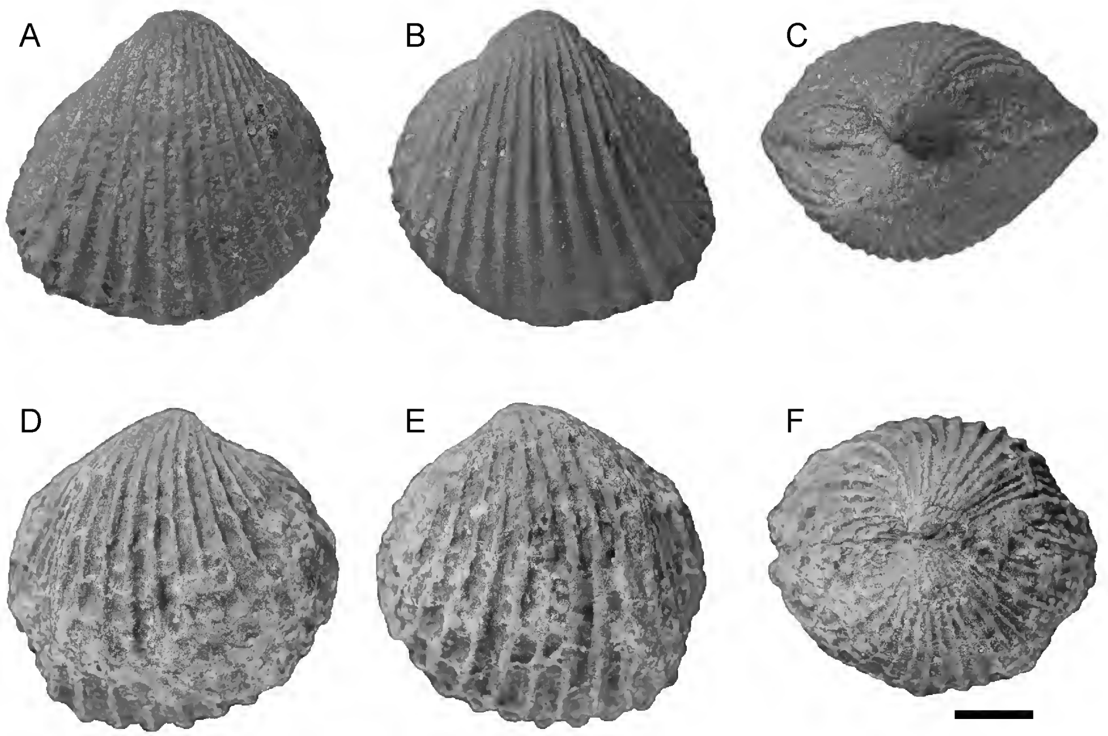


FIGURE 50. Casts (formed in situ) of Bivalvia from the Paleocene of the Teberemt Formation. Two articulated ?*Venericardia* sp.: CNRST-SUNY 178a, in **A,** right valve; **B,** left valve; and **C,** dorsal views; and CNRST-SUNY 178b in **D,** right valve; **E,** left valve; and **F,** dorsal views; and Scale bar = 5 mm.

Discussion: Unionidae are freshwater mussels (Zardus and Martel, 2002), thus these fossil specimens were likely transported into the Malian coastal sediments from nearby freshwater aquatic habitats.

ARCHIHETERODONTA Giribet in Taylor et al., 2007

CARDITOIDEA Férussac, 1822

CARDITIDAE Férussac, 1822

Venericardia Lamarck, 1801

?*Venericardia* spp.

Figure 50

Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin, and the Teberemt Formation of the Gao Trench and the Taoudenit Basin. Maastrichtian-Paleocene.

Localities: Mali-1, probably top of unit 4; Mali-7 unit 11; Mali-19, probably one of the carbonate units.

Depositional Environment: Limestone (Facies 3); possibly also shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 81, 82, 89, 100, 104, 108, $109^{7\text{-unit }11}$, 178a, b^1, $527^{19\text{-unit }2}$, 529, 539^{19}.

Description: Small subcircular to trigonal casts displaying sharp V-shaped ribs, and in some cases ventral costal nodes, an elevated beak, and a lunule. All specimens are articulated and dentition and muscle scars are not visible. Multiple species are likely.

Discussion: This taxon is commonly represented in shallow coastal settings of the Paleogene, and lived just below the sediment-water interface (Heaslip, 1968).

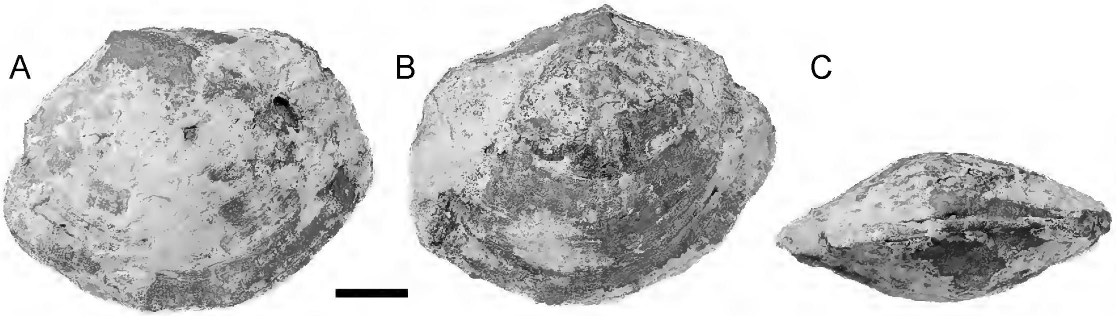


FIGURE 51. Casts (formed in situ) of Bivalvia from the Paleocene of the Teberemt Formation, Gao Trench. Articulated Lucinidae indet. (CNRST-SUNY 516), with matrix obscuring some external shell sculpture, in **A,** left valve; **B,** right valve; and **C,** dorsal views. Scale bar = 1 cm.

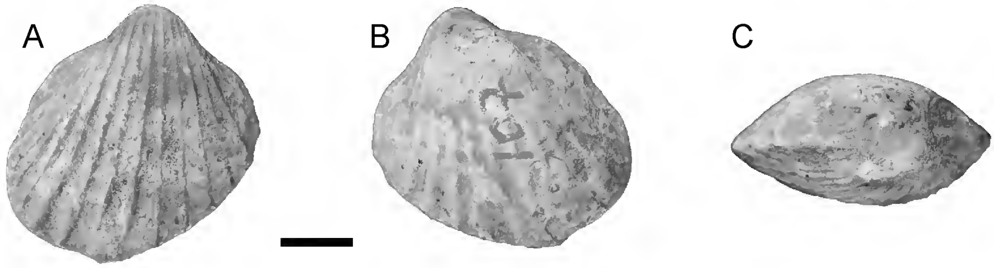


FIGURE 52. Cast (formed in situ) of Bivalvia from the Maastrichtian Ménaka Formation, Iullemmeden Basin. Articulated Cardiidae indet. (CNRST-SUNY 107) in **A,** right valve; **B,** left valve; and **C,** dorsal views. Scale bar = 5 mm.

IMPARIDENTIA Bieler et al., 2014

LUCINIDA Gray, 1854

LUCINIDAE Fleming, 1828

Lucinidae indet.

Figure 51

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded marl and shale (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 516.

Description: Articulated cast with small beak, suggestion of a depressed lunule, fine concentric bands and faint ribs.

CARDIOIDEA Lamarck, 1809

CARDIIDAE Lamarck, 1809

Cardiidae indet.

Figure 52

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-7 unit 11.

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 107.

Description: Fairly inflated shell with prominent beak. Specimen articulated, limiting identification.

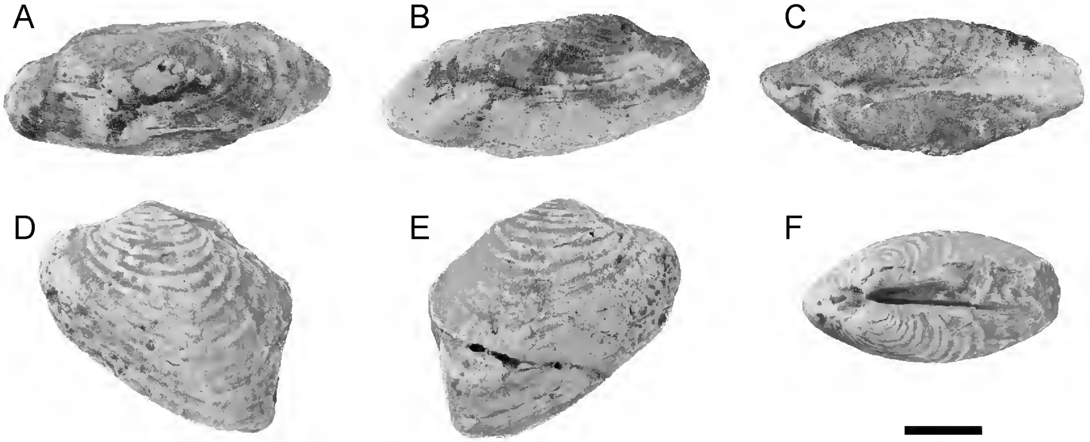


FIGURE 53. Casts (formed in situ) of articulated Bivalvia from the Paleocene of the Teberemt Formation. *Raetomya schweinfurthi* (CNRST-SUNY 544) from the Taoudenit Basin in **A,** left valve; **B,** right valve; and **C,** dorsal views; and ?*Raetomya schweinfurthi* (CNRST-SUNY 545) from the Gao Trench in **D,** left valve; **E,** right valve; and **F,** dorsal views. All specimens articulated. Scale bars = 1 cm.

Discussion: The Cardiidae have a temperate to tropical distribution and are found predominantly in shallow coastal waters (Mikkelsen and Bieler, 2008).

MYIDA Stoliczka, 1870

MYOIDEA Lamarck, 1809

RAETOMYIDAE Newton, 1919

Raetomya schweinfurthi Mayer-Eymar, 1887

Figure 53

Horizons in Study Area and Age: Teberemt Formation of the Gao Trench and the Taoudenit Basin and the Tamaguélelt and Teberemt formations of the Iullemmeden Basin. Paleocene-Eocene boundary–Eocene.

Localities: Mali-11 unit 3; Mali-16 and Mali-17 both unit 3; Mali-21.

Depositional Environment: Shale (Facies 2) interpreted as shallow, normal-to-restricted marine lagoons and open platform settings and interbedded shale and marl (Facies 4) interpreted as shallow, sublittoral open marine settings with water depths <50 m.

Referred Material: CNRST-SUNY 144^{11}, 543^{16}, 544$^{17\text{-unit }3}$, 545-546 (11 specimens)^{21}.

Description: Shell inequilateral, obliquely gibbose, slightly gaping; umbonal areas arched. Presence of mostly regular concentric ridges.

Discussion: Well illustrated in Newton et al. (1922). Raetomyidae are found in modern seas that are tropical and temperate (Mikkelsen and Bieler, 2008). Specimens CNRST-SUNY 544–545 are tentative attributions.

VENERIDA Gray, 1854

VENERIDAE Rafinesque, 1815

CALLOCARDIINAE Dall, 1895

Callocardiinae indet.

Figure 54

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-16 unit 2.

Depositional Environment: Limestone (Facies 3); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

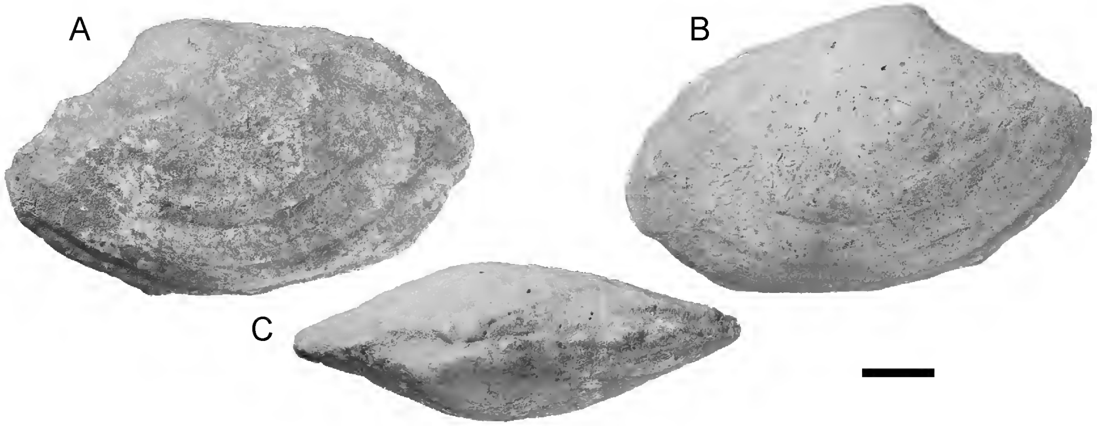


FIGURE 54. Cast (formed in situ) of articulated Bivalvia from the Paleocene of the Teberemt Formation, Gao Trench. Callocardiinae indet (CNRST-SUNY 520) in **A,** left valve; **B,** right valve; and **C,** dorsal views; Scale bar = 1 cm.

Referred Material: CNRST-SUNY 520.

Description: Elongated articulated cast with strong concentric bands preserved; impression of lunule suggested.

VERTEBRATA Lamarck, 1801

CHONDRICHTHYES Huxley, 1880

ELASMOBRANCHII Bonaparte, 1838

LAMNIFORMES Berg, 1958

CRETOXYRHINIDAE Glickman, 1958

Serratolamna (*Cretalamna*) *maroccana*
Arambourg, 1935

Figure 55A, B

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-7 unit 14.

Depositional Environment: Shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 46–49; 51–52.

Description: Isolated teeth approximately 2 cm wide and 1.5 cm tall with an asymmetrical central cusp. The central cusp is inclined distally and is slightly convex mesially. The distal margin is relatively straight. The central cusp is flanked by two cusplets on the mesial and distal sides. The proximal cusplets are significantly larger than the distal cusplets. Root lobes are asymmetrical, short, and worn to the point that no nutrient groove is visible even though roots are V-shaped.

Discussion: *Cretalamna* (= *Cretolamna* of Cappetta, 2012) is a genus of shark found in Maastrichtian and Danian rocks in many parts of the world (Underwood and Mitchell, 2000). *Cretalamna maroccana* was informally synonymized as *Serratolamna maroccana* by Belben et al. (2017) and the subject of its nomenclature was previously discussed by Underwood and Mitchell (2000) and Case and Cappetta (1997). Following personal communication with C.J. Underwood, here we formally synonymize *Serratolamna maroccana* (= *Cretolamna maroccana*; *Cretalamna maroccana*). *Serratolamna maroccana* is represented by reasonably large, robust teeth that are distinct morphologically and morphometrically from more recent lamniform sharks (Belben et al., 2017). *S. maroccana* is an index fossil and its placement at locality Mali-7 unit 14 helps define the upper

Maastrichtian part of the section. *Serratolamna maroccana* is the only nonbatoid elasmobranch identified in Mali by reasonably large, robust teeth that are distinct morphologically and morphometrically from more recent lamniform sharks (Belben et al., 2017).

BATOMORPHII Cappetta, 1980

SCLERORHYNCHIFORMES Kriwet, 2004

SCLERORHYNCHIDAE Cappetta, 1974

Schizorhiza Weiler, 1930

Schizorhiza stromeri Weiler, 1930

Figure 55C, D

Horizon in Study Area and Age: Ménaka of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-7 unit 10; Locality C. Locality C is directly south of the main locality Mali-7.

Depositional Environment: Shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: Isolated rostral teeth, CNRST-SUNY 53a and 94.

Description: The tooth crowns of the collected specimens form a small arrow tip that is compressed proximal to the neck of the root. Crown edges are sharp and lack serrations. The root is two or three times longer than the crown and bifurcates dorsoventrally. The bifurcated roots are fragmentary and indicate there would have been comblike proximal insertions.

Discussion: *Schizorhiza stromeri* is a species that was widespread across Africa, having been described originally from Maastrichtian phosphate deposits of Egypt (Weiler, 1930; Arambourg and Signeux, 1952), and later from similar-age deposits of Nigeria (White, 1934) and Congo (Dartevelle and Casier, 1943). It was documented in sediments at the base of Locality C of the Maastrichtian unit, Mali-7 unit 10 by Claeson et al. (2010) and, along with *Onchopristis numidus*, is one of two examples of sawfish batoids in the Cretaceous of Mali.

Onchopristis Stromer, 1917

Onchopristis numidus Haug, 1905

Figure 55E

Horizon in Study Area and Age: Ménaka and Teberent formations of the Iullemmeden Basin. Possibly Late Maastrichtian-Paleocene.

Localities: Mali-7 and Mali-11.

Depositional Environment: Shale and limestone (facies 2 and 3) interpreted as shallow, normal-to-restricted marine lagoons and open platform settings and small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: Isolated rostral denticle, CNRST-SUNY 53b–d^{7}, 62^{11}.

Description: Long, curved crown with asymmetrical barblike hook. The crown is widest at its broad, flat base.

Discussion: *Onchopristis* is a cosmopolitan genus of sawfish known from the lower Cretaceous to the middle Cretaceous (Kriwet and Kussius, 2001; Wueringer et al., 2009). Often known exclusively from its rostral denticles, it is used as an index taxon for vertebrate assemblages of fluvial sequences for the Aptian/Albian to Cenomanian of Egypt, Libya, Algeria, and Morocco (Rage and Cappetta, 2002; Martill and Ibrahim, 2012). Campanian records of *Onchopristis* are considered questionable (Rage and Cappetta, 2002). Currently we have poor field records regarding the stratigraphic layer in which this taxon was collected. Expanded collecting of this taxon has the potential to contribute to the biostratigraphic correlation in Malian Cretaceous rocks.

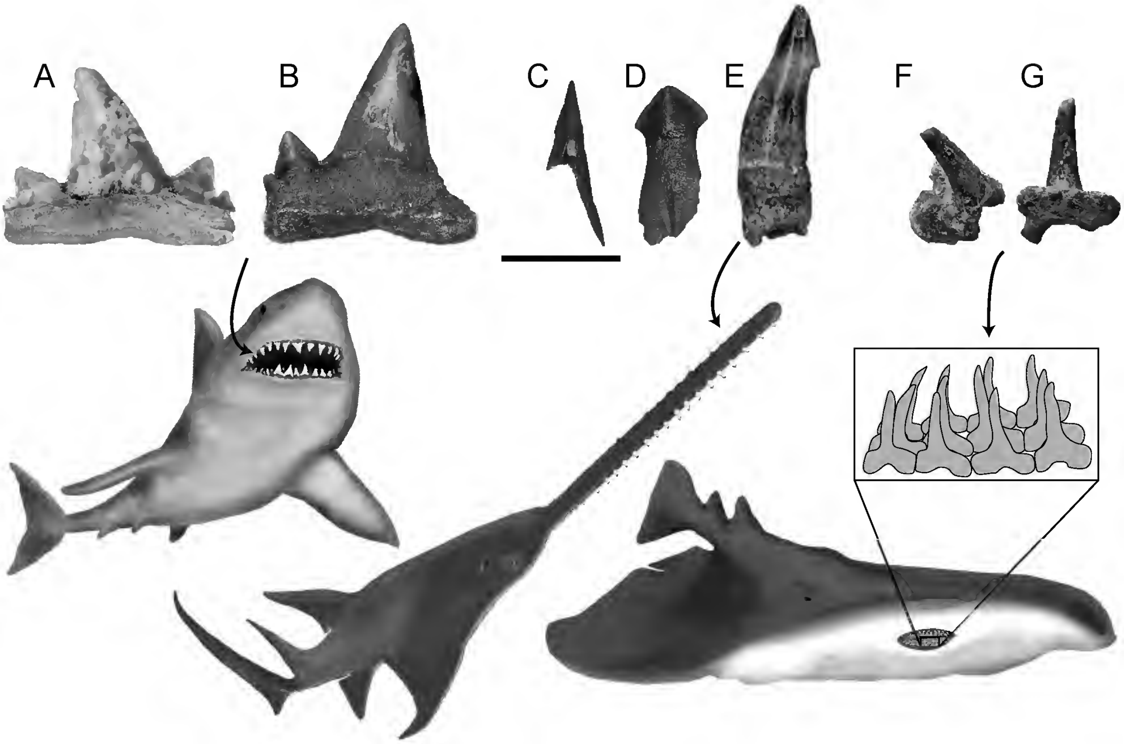


FIGURE 55. Fossil teeth of Chondrichthyes and reconstructions of the animals: shark, *Serratolamna* (*Cretalamna*) *maroccana*, isolated teeth **A,** CNRST-SUNY 46 and **B,** CNRST-SUNY 47; sawfish shark *Schizorhiza stromeri*, rostral tooth (CNRST-SUNY 94) in **C,** anterior and **D,** dorsal views; sawfish shark *Onchopristis numidus*, rostral tooth (CNRST-SUNY 53c) in **E,** dorsal view. A–E from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. An electric ray, *Eotorpedo hilgendorfi* (CNRST-SUNY 415), from the Paleocene of the Teberemt Formation, Gao Trench in **F,** occlusal and **G,** labial, views. Scale bar for tooth photos = 1 cm.

TORPEDINIFORMES de Buen, 1926

TORPEDINIDAE Bonaparte, 1838

Eotorpedo White, 1934

Eotorpedo hilgendorfi Jaekel, 1904

Figure 55F, G

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Localities: Mali-17 unit 2.

Depositional Environment: Shale (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: Isolated tooth, CNRST-SUNY 415.

Description: Single, unicuspid tooth. Crown base is flat and a single, tall, narrow cusp projects lingually and is somewhat curved. At the base of the tooth, four lobes are indicated, though one of the labial roots is fractured. Lingually positioned lobes are bulbous with a medial notch. Labially positioned lobes are more rodlike.

Discussion: Teeth of *Eotorpedo hilgendorfi* were first recovered from the upper Paleocene of Gada, Nigeria (White, 1934; Arambourg and Signeux, 1952). They have since been recovered widely throughout the Paleocene and were also recovered from the Danian and Thanetian of Northwestern Africa as reviewed in Marramà et al. (2017). The presence of *Eotorpedo hilgendorfi* in unit 2 of Mali-17 sets the upper limit of this sequence at the Thanetian (post-Danian) or latest Paleocene.

MYLIOBATIFORMES Compagno, 1973

MYLIOBATIDAE Bonaparte, 1838

Myliobatis Cuvier, 1816

Myliobatis wurnoensis White, 1934

Figure 56

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-8 unit 10.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: Isolated teeth and articulated tooth plates. CNRST-SUNY 2–18 and 37–39.

Description: Materials collected from Mali-8 include associated upper and lower partial dental plates. Partially complete plates possess six-sided and tightly interlocking teeth. Median teeth are approximately four to five times wider than they are anteroposteriorly long. In occlusal view, median teeth are straight to moderately arcuate and not distinctly chevron shaped. Lateral terminals of the median teeth are angled and pointed anteriorly, so that the curvature of median teeth is concave. Lower median teeth are less arcuate than the upper median teeth. Lateral teeth are not preserved on any specimens, but the angular, interdigitating lateral margins are retained on the median teeth for several specimens. The crown of the median teeth is thickest in the center and slopes steeply toward the lateral margins that are thin and pointed or pinched. Roots are polyaulacorhizous with 14–24 laminae. Laminae are rectangular and blocklike. Individual laminae vary in width, from 1.0–3.2 mm, and all are wider than the adjacent grooves between them. Laminae are narrow and uniform medially, with some wider and irregular laminae occurring laterally.

Discussion: *Myliobatis wurnoensis* differs from *M. dixoni* in exhibiting a pinched lateral margin of median teeth with steep lateral slopes with irregular and blocky root laminae. Malian specimens of *M. wurnoensis* represent the only well-preserved upper and lower dentitions of the taxon from the Mesozoic (Claeson et al., 2010). The prior earliest-documented occurrence of the species was the Paleocene-Landenian (White, 1934; Arambourg and Signeux, 1952; Geyter et al., 2006)

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Woodward, 1901a

NEOPTERYGII Regan, 1923

PYCNODONTIFORMES Berg, 1937

PYCNODONTIDAE Agassiz, 1833–1844

Pycnodus Agassiz, 1833–1844

Pycnodus jonesae Longbottom, 1984

Figure 57A, B

Horizons in Study Area and Age: Teberemt Formation of the Iullemmeden Basin and the Gao Trench. Maastrichtian-Paleocene.

Localities: Mali-7, Mali-8, and Mali-10; Mali-19 unit 2.

Depositional Environment: For Mali-19, phosphate conglomerate (Facies 5); shallow marine-to-brackish water phosphorites. We currently have poor stratigraphic control for the other localities, but these specimens appear to have also been preserved in marls, shales, and limestones.

Referred Material: Isolated teeth, CNRST-SUNY 54^{7}, 356^{8}; prearticular dentition, CNRST-SUNY 343^{8}, 351^{8} indeterminate tooth plates, 352 and 355^{19}, and 449c^{10}.

Description: Upper and lower dentitions with white to blue tooth crowns. Symmetrical vomerine elements with a median toothrow of broad crowned teeth. Lateral vomerine teeth are more round than broad. Asymmetrical preartic-

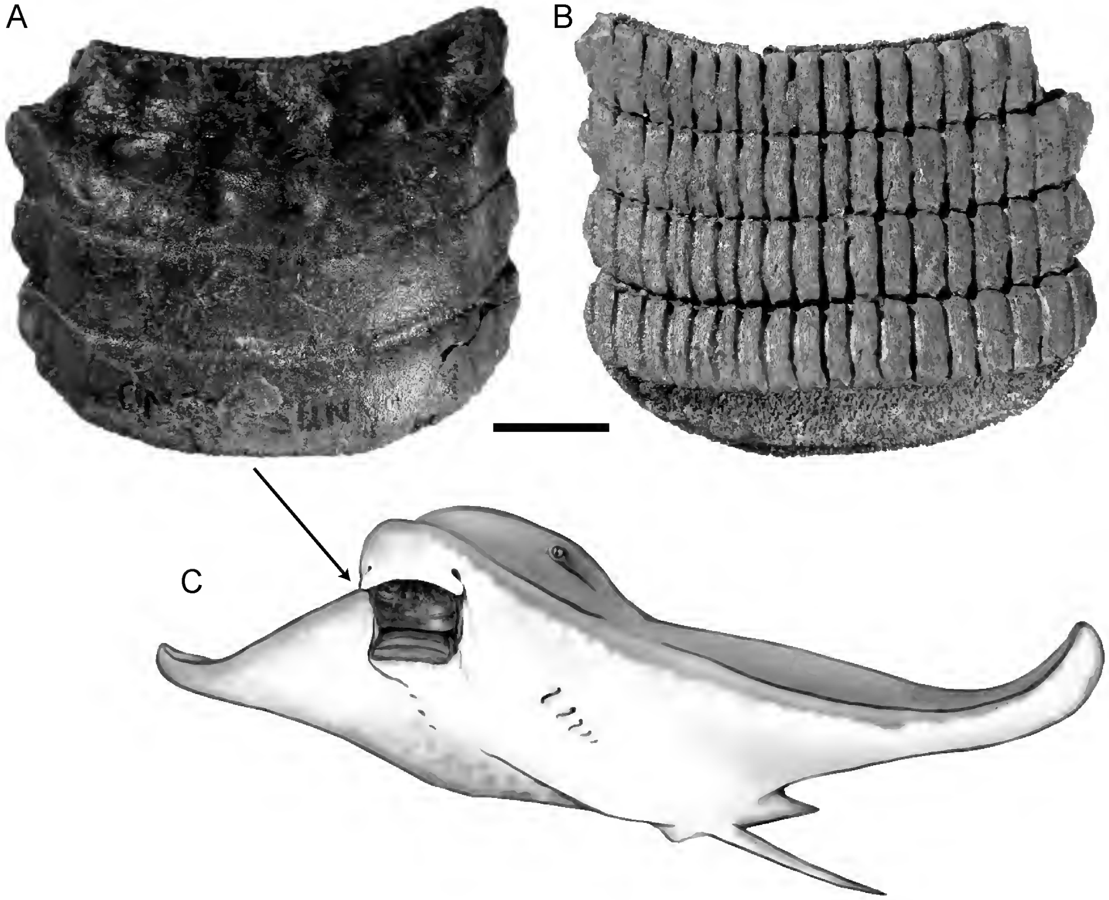
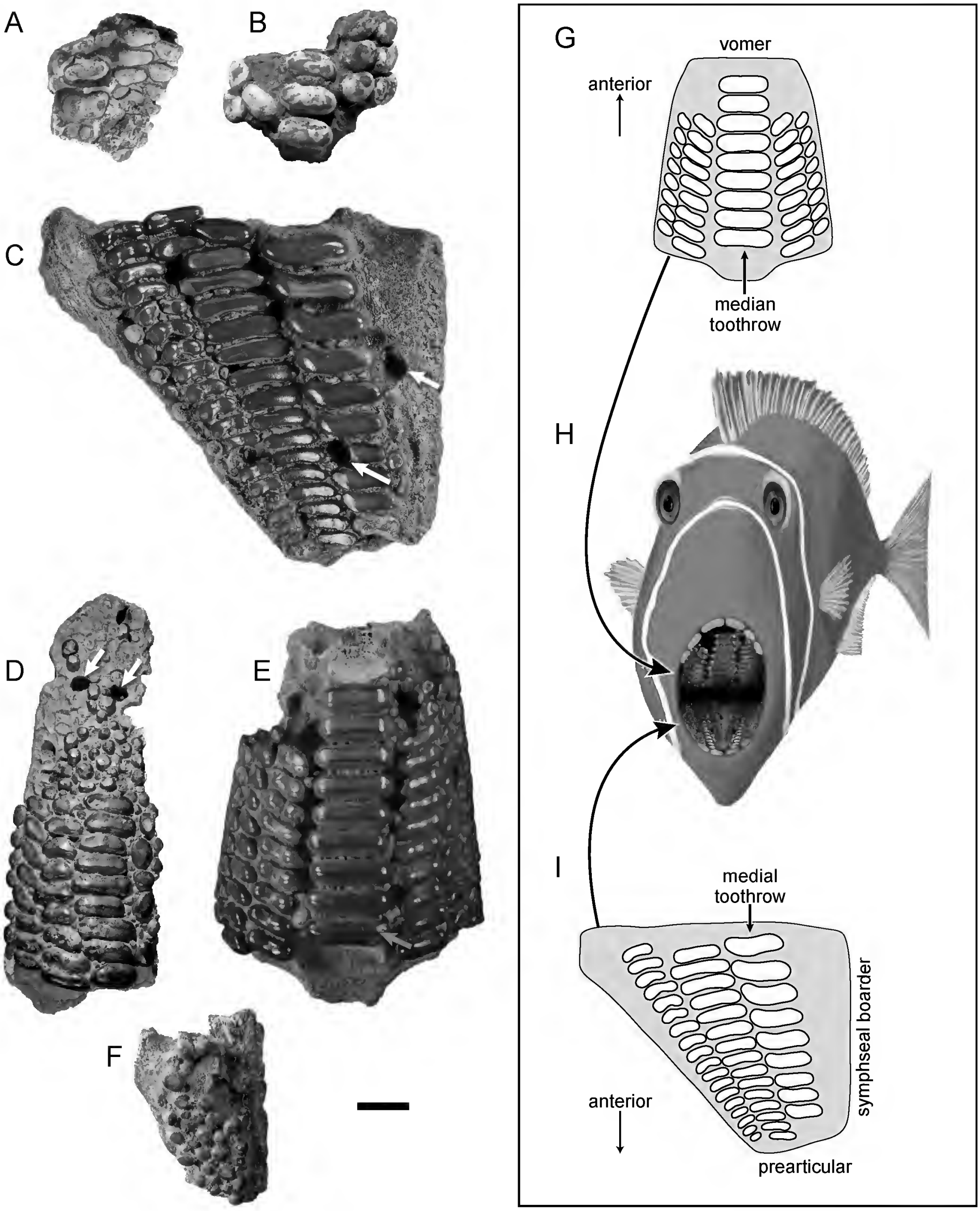


FIGURE 56. Fossil tooth plate and reconstruction of the stingray *Myliobatis wurnoensis* (Chondrichthyes, Myliobatiformes) from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. CNRST-SUNY 37, tooth plate in **A,** occlusal and **B,** root views; and **C,** reconstruction of *M. wurnoensis* showing position of tooth plate in mouth. Scale bar = 1 cm.

ular bones with medial and first lateral toothrows bearing relatively equal-sized crowns.

Discussion: Pycnodontidae contains species that have cusped teeth (such as *Stephanodus*, discussed below), where the teeth are compressed and taper to a pointed hook, and species that are noncusped, that is, those for which each tooth is a simple convex surface. All the Malian species of noncusped pycnodonts were previously considered to be from the genus *Pycnodus* (Longbottom, 1984) and we follow this attribution here. *Pycnodus jonesae* is distinct from other Malian taxa in having median teeth that are 2–5× times as wide as long, and oval lateral teeth. *P. jonesae* is the only species of *Pycnodus* from Mali found in the Maastrichtian sediments. New specimens of *Pycnodus jonesae* are preserved differently than other Malian species of *Pycnodus* in having white tooth crowns instead of shiny dark-brown crowns.

We have several pycnodont species from Mali and here we briefly discuss some broader evolutionary patterns that apply to the clade. Pycnodonts were a mostly marine family that reached maximum diversity during the Cretaceous in the Western Tethys (Poyato-Ariza and


A
B
C
D
E
F
G
vomer
anterior
median
toothrow
H
I
medial
toothrow
symphseal boarder
anterior
prearticular

Martín-Abad, 2013), a sea that would have directly communicated with the Trans-Saharan Seaway from the north, and may have been a route for many pycnodonts to travel into and out of the inland epeiric sea. Poyato-Ariza and Martín-Abad (2013) produced a species-level phylogeny calibrated with ghost lineages that drew on older work (Poyato-Ariza and Wenz, 2002; Kriwet, 2005) and showed at least four major lineages crossing the K-Pg boundary. That study did not include the diverse African species. North and South American forms became extinct before the Maastrichtian, and the entire clade became extinct by the early-middle Eocene (Poyato-Ariza and Martín-Abad, 2013). This pattern suggests that pycnodonts in Africa survived later than those in South America did, and that Mali preserves some of the latest-surviving pycnodonts. Paleocene pycnodonts in Mali were relatively small compared to Eocene forms suggesting there may have been a body size increase in this clade through time.

Pycnodus is found on both sides of the K-Pg boundary in our section. Cavin and Martin (1995) observed that shallow water marine actinopterygians like pycnodonts were more severely impacted by the K-Pg boundary than deepwater species, but nonetheless survived this event. Some pycnodont fossils come from nonmarine rocks and Cavin and Martin (1995) speculated that an ability to exploit both freshwater and marine habitats may have aided pycnodonts in their survival.

Pycnodus maliensis Longbottom, 1984

Figure 57C

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20 unit 2.

Depositional Environment: Phosphate conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: Prearticular dentition, CNRST-SUNY 266, 344, 449b.

Description: Asymmetrical prearticular bone with multiple toothrows of dark-brown shiny teeth. Medial (innermost) toothrow has largest teeth. Medial teeth are broad and often slightly curved and depressed in the middle. Lateral teeth are mostly broad and can be numerous in some cases, interpreted to be a pathological condition—i.e., a single row of teeth becomes an irregular patch of smaller, buttonlike teeth.

Discussion: One of three noncusped pycnodont species of the genus *Pycnodus* described by Longbottom (1984). Further study may indicate that these specimens represent the lower dentitions of *P. zeaformis*, a taxon with teeth of similar size and shape as described by Longbottom (1984). Conclusive discriminatory evidence would require finding the upper and lower dentitions as part of a complete skull. We note that coordinates for the specimens from Longbottom (1984) and for these new specimens collected during our 2003 field season indicate that the specimens were collected in close proximity.

FIGURE 57. Fossil dentitions of *Pycnodus* species in occlusal views. *Pycnodus jonesae*, **A,** CNRST-SUNY 351, left prearticular dentition from the Maastrichtian of the Ménaka Formation, and **B,** CNRST-SUNY 352, a vomerine dentition from the Paleocene of the Teberemt Formation. **C,** *Pycnodus maliensis*, right prearticular dentition, CNRST-SUNY 266 from the Eocene of Tamaguélelt Formation of the Taoudenit Basin; **D,** *Pycnodus zeaformis*, CNRST-SUNY 346 and **E,** CNRST-SUNY 265, both vomerine dentitions from the Eocene of Tamaguélelt Formation, Taoudenit Basin, and **F,** CNRST-SUNY 348, a prearticular dentition (left side, horizontally flipped in figure). **G,** generalized view of prearticular dentition for comparison with A, C and F, **H,** reconstruction of a pycnodont fish in anterior view showing in situ positions of dentitions, and **I,** generalized view of vomerine dentition, for comparisons with B, D, and E. Size of *P. zeaformis* fossil suggests a body length more than 1 m, making it one of the largest pycnodonts ever described. Red arrow indicates tooth used for body-size reconstruction (see text). White arrows indicate bored holes of ichnospecies *Gastrochaenolites ornatus.* Scale bar = 1 cm (C–E share a scale bar).

Pycnodus zeaformis (Longbottom, 1984)

Figure 57D–I

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20 unit 2 (lower phosphates).

Depositional Environment: Phosphate conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: Vomerine dentitions CNRST-SUNY 265, 345, 346, 349, 350.

Description: Symmetrical vomer with multiple toothrows. Median toothrow has largest teeth. Teeth are broad, slightly depressed in the middle, and not curved. Two rows of broad lateral teeth flank the median row. On some specimens, the anteriormost aspect of the vomer has an irregular patch of smaller, buttonlike teeth.

Discussion: One of three noncusped pycnodont species of the genus *Pycnodus* (Longbottom, 1984). It should be further examined whether these specimens represent the upper dentitions of *P. maliensis*. Pycnodontid fishes, many of which are preserved as full bodies, typically have relatively small body length in the range of 25 cm or less (Poyato-Ariza and Wenz, 2002; Shimada et al., 2010). Body size of pycnodont fishes has been estimated using dentitions when other skeletal elements are not available, and some pycnodonts have been estimated to have had a body length as large as 1.5 m (e.g., *Hadrodus*). The large end of this range is represented by the North American pycnodont *Macropycnodon* (Kriwet and Schmitz, 2005; Shimada et al., 2010). The body length estimates of *Macropycnodon* were made by comparing its median vomerine tooth length with that of the pycnodont genus, *Coelodus*, because the entire skeleton of *Coelodus* is known (Shimada et al., 2010). The median vomerine tooth size of *Coelodus* is approximately 0.5 cm in width and the total length of the *Coelodus* body is 35 cm. Based on that ratio, Shimada et al. (2010) predicted *Macropycnodon* would reach 122 cm total length.

The median vomerine teeth of the Malian pycnodonts that we collected and that are described here reach nearly 1.75 cm in width, thus wider than the 1.1 cm median vomerine tooth size for other Malian pycnodonts published by Longbottom (1984). Using such teeth and the method of Shimada et al. (2010; i.e., measuring the width of the most posterior median vomerine tooth) we estimate that *Pycnodus zeaformis* ranged between 77 cm (based on CNRST-SUNY 346) and 122 cm (based on CNRST-SUNY 265), and conclude that this Malian taxon was a relative giant among pycnodonts. The larger estimate comes from a tooth in the dentition of CNRST-SUNY 265 indicated in figure 58C.

Pycnodus sp.

Horizons in Study Area and Age: Maastrichtian-Eocene, or possibly lower Eocene, of Ménaka and Teberemt formations of the Iullemmeden Basin and the Tamaguélelt Formation of the Taoudenit Basin.

Localities: Mali-8; Mali-11; Mali-20.

Depositional Environment: Phosphate conglomerate (Facies 5); shallow marine-to-brackish water phosphorites. We have poor control of stratigraphy and facies change for the beds of Mali-11, but it appears that marls, shales, and limestones also yield these specimens.

Referred Material: CNRST-SUNY 58^{11}, 347, 348, 353, 354^{20}, $374c^{8}$, 384d, fragmentary dental specimens often preserving partial jaws.

Description: These specimens have generic level similarities to pycnodonts (features noted above) but are too fragmentary to assign to species.

Stephanodus lybicus (Dames, 1883)

Figure 58A–C

Horizons in Study Area and Age: Ménaka and Teberemt formations of the Iullemmeden Basin. Maastrichtian through Paleocene.

Localities: Mali-7, top of unit 13; Mali-11.

Depositional Environment: For Mali-7, limestones (Facies 3) interpreted as small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity; for Mali-11, shales and limestones (facies 2 and 3); interpreted as the same as just mentioned for Mali-7 as well as shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: isolated teeth CNRST-SUNY 43, 45, 56, 57, 814, 815^{7}; 95, 97a$^{7\ \mathrm{loc.\ C}}$, 138$^{7\ \mathrm{unit\ 13}}$; 69, 70^{11}.

Description: Cusped, hooklike enameloid teeth.

Discussion: The hook-shaped teeth assigned to *Stephanodus libycus* were previously found in the branchial chamber of pycnodont fishes (Kriwet, 1999). Similar isolated teeth have also been attributed to the Eotrigonidae, Tetraodontiformes in the Eocene (White, 1934) and the Maastrichtian (Cappetta et al., 2014). We follow Lourembam et al. (2017) who argued in his more recent work on faunas contemporary to the Malian fauna that *Stephanodus* remains represent a pycnodontiform taxon. The specimens previously described by White (1934) were from the Upper Cretaceous of the Nigerian Sokoto Province; the Malian specimens extend that range into the Paleocene.

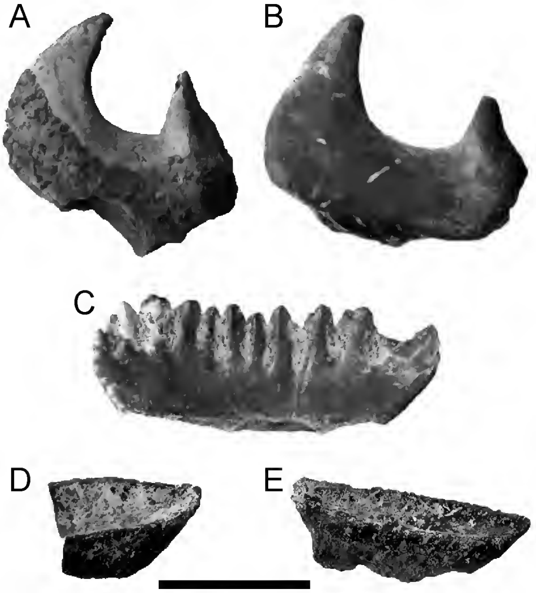


FIGURE 58. Dentitions of fossil actinopterygians from the Iullemmeden Basin, Mali. *Stephanodus lybicus*, **A**, CNRST-SUNY 815 and **B**, CNRST-SUNY 814, both pharyngeal teeth, and **C**, CNRST-SUNY 95, an oral tooth, all from the Maastrichtian of the Ménaka Formation; and *Eotrigonodon*, **D**, CNRST-SUNY 812, and **E**, CNRST-SUNY 813, both oral upper teeth from the Paleocene of the Teberemt Formation. Scale bar = 1 cm.

TETRAODONTIFORMES Berg, 1937

Eotrigonodon jonesi White, 1934

Figure 58D, E

Horizon in Study Area and Age: Teberemt Formation of the Iullemmeden Basin. Paleocene.

Locality: Mali-11.

Depositional Environment: Interbedded limestone and paper shale (facies 2 and 3) interpreted as shallow, normal-to-restricted marine lagoons and open platform settings and small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 60b, 812, 813, all upper oral teeth.

Description: Approximately 25 spatulate oral teeth, most with a crown approximately 0.5 cm wide.

Discussion: White (1934) named this poorly understood taxon based on similar fossils found in the Eocene Sokoto Province deposits of Nigeria; the Malian specimens represent a younger occurrence.

HALECOSTOMI Regan, 1923

AMIIFORMES Hay, 1929

AMIIDAE Bonaparte, 1838

VIDALAMIINAE Grande and Bemis, 1998

Maliamia Patterson and Longbottom, 1989

Maliamia gigas Patterson and Longbottom, 1989

Figure 59

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20, probably unit 2.

Depositional Environment: Phosphate conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 268, 387, 387b, 387c, 387d, 692, all edentulous fragmentary jaws.

Description: Isolated jaw fragments including dentary and premaxilary bones, without teeth.

Discussion: The actinopterygian halecostome fish *Maliamia* is the youngest member of the clade Vidalamiinae, an entirely extinct group of bowfin fish that existed from the Early Cretaceous through the early Eocene (Grande and Bemis, 1998: fig. 433). Until a recent discovery in Senegal (O'Leary et al., 2012), *Maliamia* was the only known African species of amiid. Prior authors (Patterson and Longbottom, 1989; Grande and Bemis, 1998) have also remarked on the extremely large estimated body length of *Maliamia*, which, although based on fragmentary remains, may have been between 1.8 and 3.5 m, which would make it the largest known member of Vidalamiinae. Vidalamiinae are known from both freshwater and marine deposits found near coastal marine localities, which led Grande and Bemis (1998: 645) to posit a probable anadromous life history for the clade. The Malian species appear subsequent to the peak diversity for amiids, which occurred in the Cretaceous (Poyato-Ariza and Martín-Abad, 2013). Some have argued that the Late Cretaceous decline in amiid diversity was independent of catastrophic events related to the K-Pg boundary (Poyato-Ariza and Martín-Abad, 2013). The new specimens of *Maliamia* were recovered just a few miles from the type locality, from depositional environments consistent with a near coastal marine lifestyle.

In their comprehensive review of Amiidae, Grande and Bemis (1998: tables 80–119) reported standard length estimates for all the fossils they examined within the family. The smallest individual had a length of 5.5 cm. We found the average lengths for all the specimens they reported to be 45 cm. Grande and Bemis (1998) estimated that *Maliamia* was at least 180 cm in standard length, putting it at the maximum end of the known range.

TELEOSTEI Müller 1846

OSTEOGLOSSIFORMES Berg, 1940

OSTEOGLOSSIDAE Bonaparte, 1832

Brychaetus Woodward, 1901b

Brychaetus sp.

Figure 60

Horizons in Study Area and Age: Ménaka and Teberemt formations both Iullemmeden Basin and Tamaguélelt Formation of the Taoudenit Basin. Maastrichtian-Eocene, possibly lower Eocene.

Localities: Mali-8, probably unit 10; Mali-10 (collected as float); and Mali-20, several specimens from unit 2 specifically.

Depositional Environment: Alternating conglomeratic phosphorites (Facies 5) interpreted as shallow marine-to-brackish water phosphorites and paper shales (Facies 2) interpreted as shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 42^{8}, 131^{10}, 259–260, 390, $390b^{20,\text{ unit }2}$, 680–684, 690^{20}.

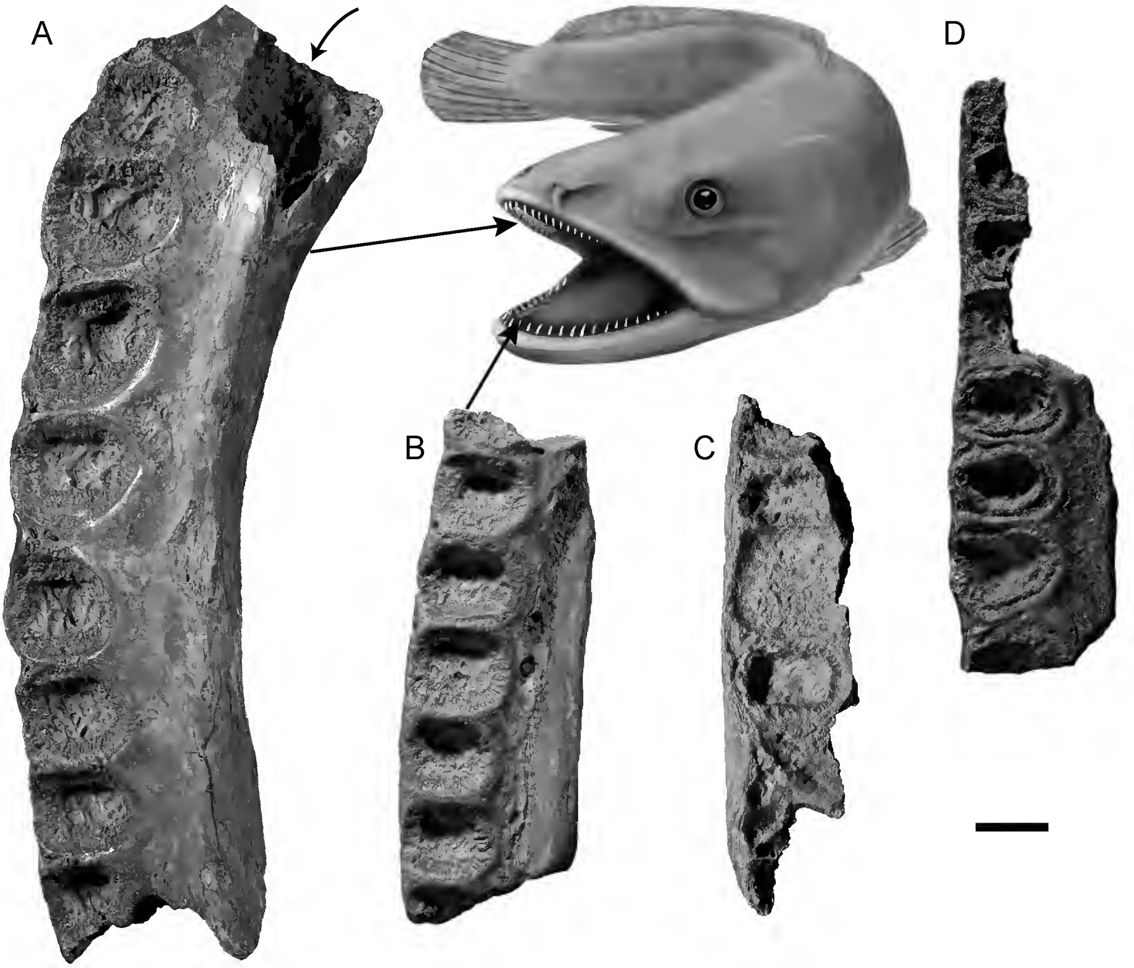


FIGURE 59. *Maliamia gigas*, from the Eocene of the Tamaguélelt Formation Taoudenit Basin, Mali. Gnathic fragments in occlusal view and reconstruction of animal. **A**, CNRST-SUNY 268, right maxilla (anterior toward top of page), curved arrow indicates large marrow chamber; **B**, CNRST-SUNY 387, right midshaft dentary fragment; **C**, CNRST-SUNY 387b middentary fragment (side indeterminate); **D**, CNRST-SUNY 387c, right posterior dorsal ramus of dentary. At the top center, reconstruction of *Maliamia gigas* showing gnathic fragments in situ. Scale bar = 1 cm.

Description: Dentary fragments with teeth, alveoli, and in one case the mandibular symphysis.

Discussion: Based only on several teeth and dentary fragments, it is not possible to identify to which species of *Brychaetus* these specimens belong (Taverne, 2009). *Brychaetus*, originally described from early Eocene marine London Clay, may also occur also in the Stolle Klint Clay in the United Kingdom, and is known from the Eocene phosphates of Morocco and Nigeria (Bonde, 2008). The Malian specimens preserve teeth of different sizes and in different positions in the jaw (compare CNRST-SUNY 259 and 684). The Maastrichtian specimen that we report is relatively gracile and appears to be the first appearance of this genus in the Mesozoic. The base of this specimen does not preserve a jaw.

A premaxillary fragment from the Iullemmeden Basin of Niger was reassigned from

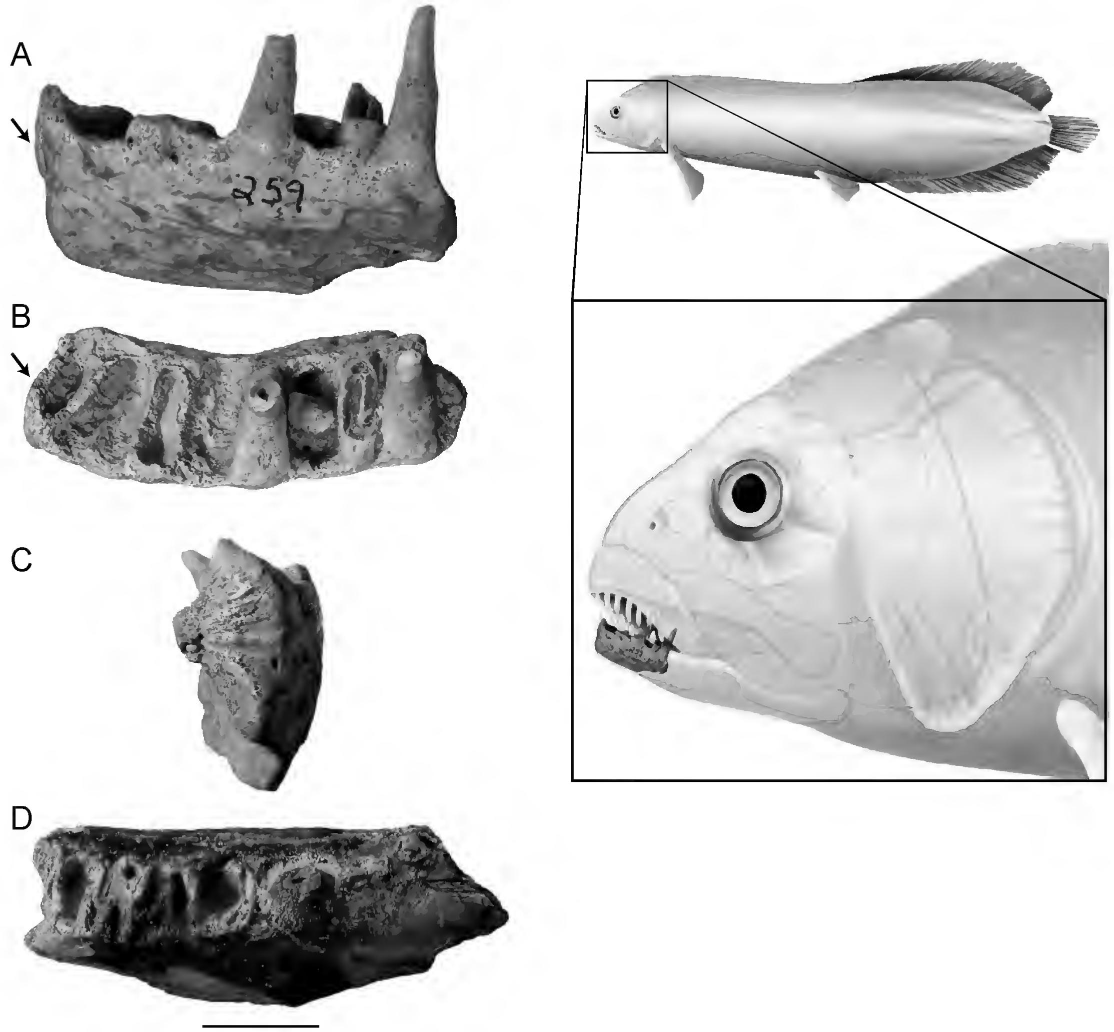


FIGURE 60. Gnathic remains of *Brychaetus* sp. CNRST-SUNY 259, a left dentary fragment from the Eocene of the Tamaguélelt Formation showing several preserved teeth in **A,** lateral; **B,** occlusal; and **C,** anterior views, the latter showing the mandibular symphysis (arrows in A and B indicate position of symphysis). **D,** CNRST-SUNY 42, an upper jaw with broken teeth from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. At right, reconstruction of the fish in life showing the position of CNRST-SUNY 259 in situ. Scale bar = 1 cm.

Brychaetus muelleri to *Scleropages africanus* (Taverne, 2009). This is the closest species geographically to the Malian specimen. Tapanila et al. (2008) cited Taverne (1974) to support the hypothesis that Malian *Brychaetus* is an unambiguously marine taxon.

SILURIFORMES Cuvier, 1816

CLAROTEIDAE Bonaparte, 1846

Nigerium White, 1934

Nigerium tamaguelense Longbottom, 2010

Horizon in Study Area and Age: Tamaguélelt Formation, Tilemsi Valley of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Tamaguélelt of the In Fargas and Cheit Keini regions.

Depositional Environment: Alternating conglomeratic phosphorites (Facies 5); shallow marine-to-brackish water phosphorites and paper shales (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: NHMUK PV P.66679–P.66707.

Description: Longbottom (2010) diagnosed a species of *Nigerium* with the following characters: fontanellar groove not reaching posterior to the pterotic; anterior part of the pterosphenoid long and pointed; vertebral complex unfused to basioccipital; and an open aortic groove.

Discussion: Freshwater catfish such as these are relatively abundant in Malian phosphates hypothesized to be early Eocene age (Tapanila et al., 2008; Longbottom, 2010). Longbottom (2010) described several Malian specimens that are the oldest members of the clade Claroteidae, which is the oldest family of catfish in Africa. Additional freshwater African catfish species come from the Late Eocene of Sokoto Province in Nigeria and are assigned to *Eaglesomia*, a clade that is not considered closely related to *Nigerium* (White, 1934; Longbottom, 2010). An extensive record of large, Eocene marine catfish from Africa also exists, including the species *Fajumia*, *Socnopea*, and *Qarmoutus* (El-Sayed et al., 2017).

Unnamed Taxon

Figure 61

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20 unit 2 (lower phosphates).

Depositional Environment: Alternating conglomeratic phosphorites (Facies 5); shallow marine-to-brackish water phosphorites and paper shales (Facies 2); shallow, normal-to-restricted marine lagoons and open platform settings.

Referred Material: CNRST-SUNY 383d, 384, 384b–c, 385a–c (see also Tapanila et al., 2008).

Description: Multiple isolated vertebrae and vertebral complexes of varying size. The largest vertebral complex is over 8 cm in length. All vertebral complexes include an open aortic canal and appear fused to the basioccipital.

Discussion: The recovered examples of the Weberian apparatus of this undescribed Malian taxon all possess an open aortic canal and are thus tentatively placed along with *Nigerium tamaguelense* within the clade Claroteidae. The open aortic canal means the new taxon differs from contemporary Egyptian fossil taxa, all of which have closed aortic canals. The new Malian taxon, which was also presumably freshwater, as discussed above for *N. tamaguelense*, is also larger than any other African catfish, including the giant sea catfishes (Ariidae) from the Eocene of Egypt (El-Sayed et al., 2017). It occurred much later than the freshwater endemic mochokid catfish from the Miocene of Chad (Pinton et al., 2011). We conducted ratio comparisons of vertebral complex length to full body length to provide preliminary estimates of the body size of the new taxon. For the extant catfish, *Clarotes laticeps* (ANSP 77912), this ratio is 5 cm:40 cm. By

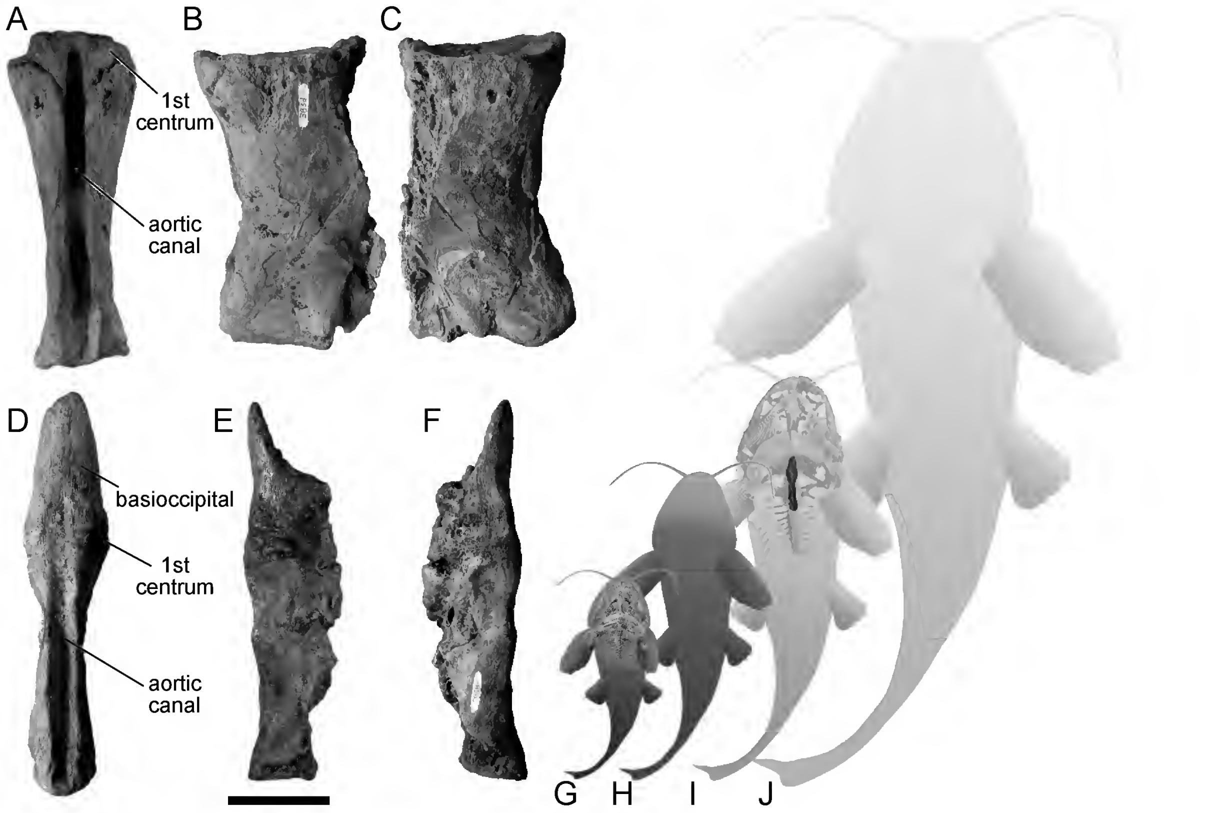


FIGURE 61. New Malian catfish specimens, Claroteidae (Siluriformes), **A–F,** from the Eocene phosphatic conglomerates of the Tamaguélelt Formation, Taoudenit Basin, Mali, with modern and fossil comparisons indicating the relatively large size of the new specimens. Two examples of the vertebral complex of the new unnamed taxon: CNRST-SUNY 383d, in **A,** ventral; **B,** left lateral; and **C,** right lateral views; and CNRST-SUNY 385a, in **D,** ventral; **E,** left lateral; and **F,** right lateral views; **G–J,** comparative full-body reconstructions in ventral view and total length estimates (see text): **G,** extant *Clarotes laticeps* (ANSP 77912) with skull shown in situ, 40 cm long; **H,** *Nigerium tamaguelense* from the Paleogene of the Tilemsi Valley, Mali, described by Longbottom (2010), 80 cm long; **I,** CNRST-SUNY 385a, 104 cm long, fossil in **D** shown in situ superimposed over skull of an extant catfish; and **J,** CNRST-SUNY 383d, 160 cm long. The extant species is freshwater and the Malian specimens are hypothesized to have been freshwater as well. Scale for A–F = 10 cm.

the same ratio, the vertebral complex: body length estimates of the fossil catfish predict the following body sizes: *N. tamaguelense,* 10 cm:80 cm (approximated from Longbottom, 2010), CNRST-SUNY 385a, 13 cm:104 cm, and CNRST-SUNY 383d, 20 cm:160 cm. Thus, the new Malian specimens are distinctly larger than close relatives that are both extant and extinct.

The clade Claroteidae has extant members and measured total body lengths have been reported for 110 specimens in Fishbase (Froese and Pauly, 2019). The minimum reported total length for an adult was 3.4 cm, and the average, based on our average of all reported claroteid fishes is 30 cm. To estimate the body length of the largest Malian catfish, we first compared the total length of extant catfish with the length of their vertebral complex. We then extrapolated to find a total length for the new Malian catfish species using the length of its preserved vertebral complex. In an extant catfish of 40 cm in total length, the vertebral complex is approximately 5 cm long. The largest vertebral complex from Mali is 20 cm, thus we can conservatively estimate the total length of this extinct fish to have been as long as 160 cm and very large for its clade.

AULOPIFORMES Rosen, 1973

STRATODONTIDAE Cope, 1872

Stratodus apicalis Cope, 1872

Figure 62A–C

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20, specifically the lower phosphates for CNRST-SUNY 383e.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 383e, 686–689, 809, and 810.

Description: Jaw fragments that are primarily edentulous, with the exception of CNRST-SUNY 809. The jaws are slightly convex toward what is presumably the oral surface with the alveoli arranged in a nonspecific pattern and with some minor size variation. CNRST-SUNY 809 preserves part of the enameloid plate that was the chewing surface.

Discussion: This taxon was described from Maastrichtian sediments of Morocco, Mali, and Niger (Tabaste, 1963; Moody and Sutcliffe, 1991). Our specimens come from younger rocks indicating that this taxon exists on both sides of the

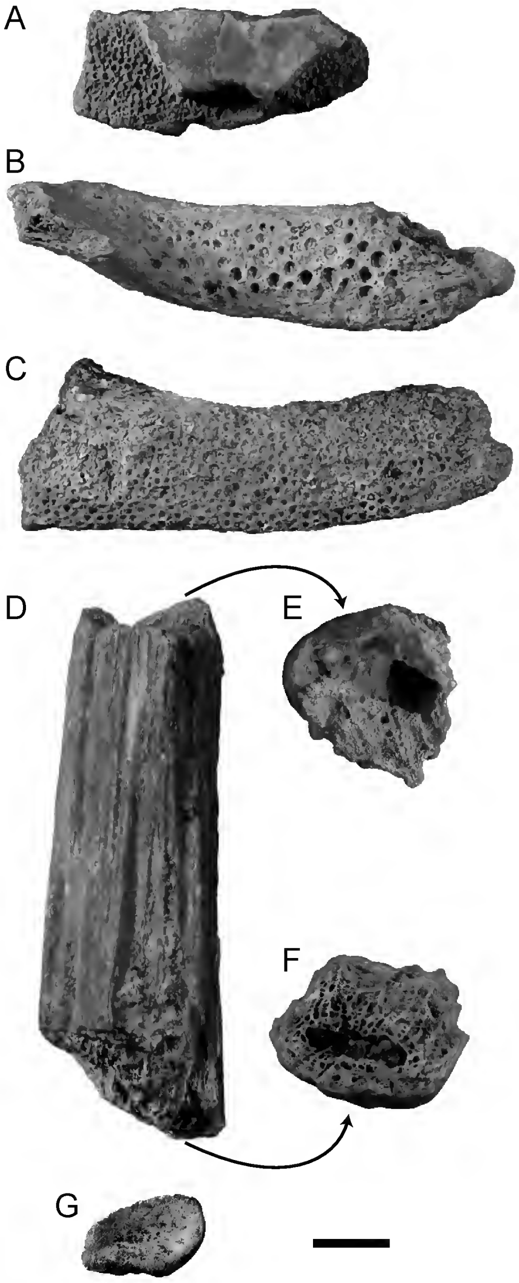


FIGURE 62. Fossil teleosts recovered from Mali. Gnathic remains of *Stratodus apicalis*: **A,** CNRST-SUNY 809 with enameloid chewing surface attached; **B,** CNRST-SUNY 689, and **C,** CNRST-SUNY 686; *Cylindracanthus* remains: **D–F,** (CNRST-SUNY 691) indicating hollow core of the structure. A–F from the Eocene Tamaguélelt Formation of the Taoudenit Basin; and **G,** an oral tooth attributed to ?Sparidae (CNRST-SUNY 816) from the Paleocene Teberemt Formation of the Taoudenit Basin. Scale bar = 1 cm.

K-Pg boundary. Cope (1872) originally identified this fossil from Kansas and it has also been reported from the Cretaceous of Alabama (Schein and Lewis, 2007).

Cylindracanthus Leidy, 1856

Figure 62D–F

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 691.

Description: Fragment of a cylindrical rod with each end broken and a hollow core. Rod is marked by ridges that extend along its full length. One end of the rod is oval in cross section and the other is gently triangular.

Discussion: Friedman (2012) discussed that it is currently still unclear whether these fossils represent spines or rostra because complete specimens of this fish taxon are still lacking. Histological comparisons of Cretaceous and Eocene *Cylindracanthus* specimens with billfishes, paddlefish, and sturgeon by Grandstaff et al. (2017) show no structural or mineralogical similarities aiding taxonomic assignment (Grandstaff et al., 2017).

PERCOMORPHI Cope, 1871

?Sparidae Rafinesque, 1818

Figure 62G

Horizons in Study Area and Age: Teberemt and Ménaka formations of the Iullemmeden Basin. Maastrichtian-Paleocene.

Locality: Mali-8, unit uncertain, and Mali-11 unit 2.

Depositional Environment: For Mali-11 (facies 2 and 3), alternating shale and limestone interpreted as shallow, normal-to-restricted marine lagoons and open platform settings and small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal marine salinity.

Referred Material: CNRST-SUNY 60a^{11}, 375b^{8}.

Description: Isolated incisiform anterior oral teeth.

Discussion: Percomorphi, previously Perciformes (sensu Johnson and Patterson, 1993) are a phylogenetically complicated group of fishes lacking synapomorphies (Wiley and Johnson, 2010). Among them, Sparidae are marine fishes (Nelson, 2006) with heterodont dentitions that include incisiform anterior oral teeth and bulbous posterior oral teeth, the latter hypothesized to have been used for crushing (Smith, 1938; Otero and Gayet, 2001). Although some have been found in northern African sediments (Arambourg and Signeux, 1952) and Niger (Michaut, 2017), we have not identified any of the posterior oral teeth of this taxon in the Malian sediments. More complete sparid specimens collected by British expeditions to Mali and Niger and housed in the NHML await description.

SARCOPTERYGII Romer, 1955

DIPNOI Müller, 1844

CERATODONTIFORMES Berg, 1940

LEPIDOSIRENIDAE Bonaparte, 1841

Lavocatodus giganteus Martin, 1995

Figure 63

Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin, Teberemt Formation of the Gao Trench, and Tamaguélelt Formation of the Taoudenit Basin. Maastrichtian-Eocene, possibly lower Eocene.

Localities: Mali-7, Mali-8, Mali-17 unit 3, Mali-19 and Mali-20, probably unit 2 (lower phosphates).

Depositional Environment: Phosphate conglomerates (Facies 5); shallow marine-to-

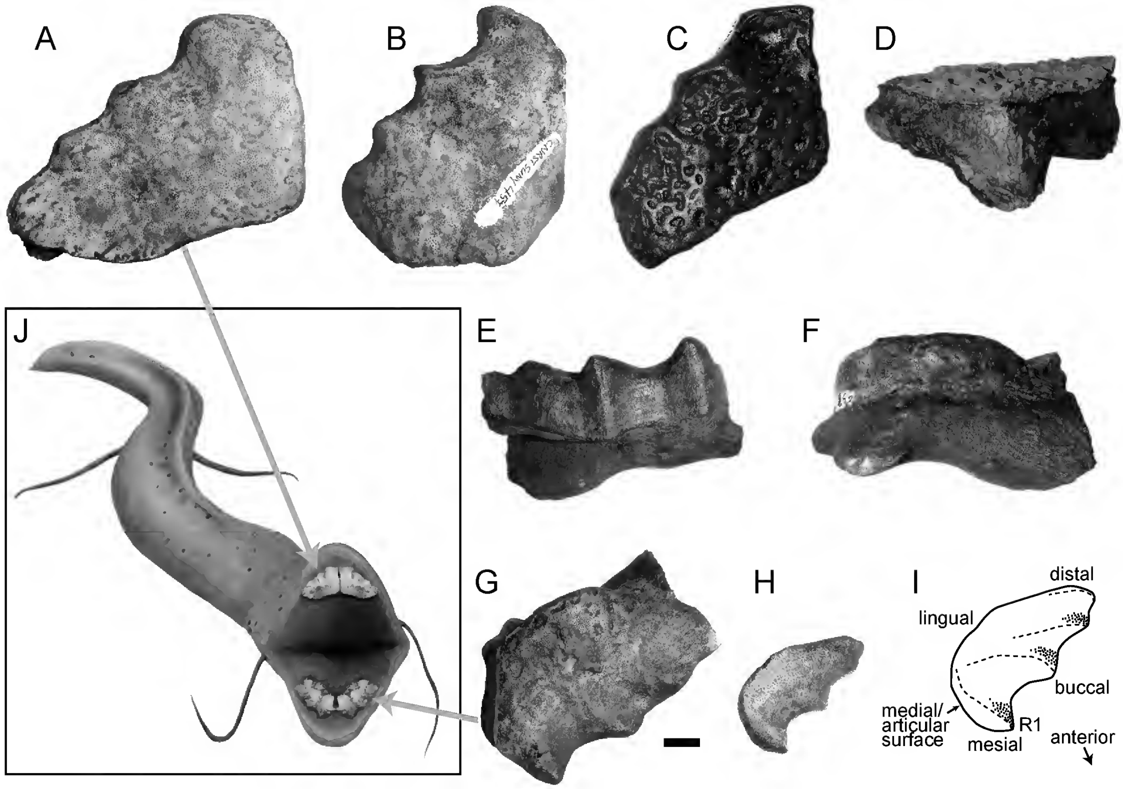


FIGURE 63. Teeth of the extinct lungfish *Lavocatodus giganteus*. Occlusal views of right pterygoid tooth plates: **A,** CNRST SUNY 456; **B,** CNRST SUNY 457; and **C,** CNRST-SUNY 191 (left side, reversed in figure); **D,** left pterygoid bone, buccal view, CNRST-SUNY 455; **E–G,** right prearticular tooth plate (CNRST-SUNY 193) in **E,** buccal; **F,** lingual; and **G,** occlusal views; **H,** left prearticular tooth plate of CNRST-SUNY 192; **I,** orientation guide to features of prearticular teeth, R1 = ridge one of four ridges shown; and **J,** reconstruction of an extinct lungfish with pterygoid and prearticular teeth in situ in mouth. A, B and D from the Paleocene of the Teberemt Formation, Gao Trench, and C, E–H from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. Scale bar for A–H = 1 cm.

brackish water phosphorites and interbedded marl and shale (Facies 4); shallow, sublittoral open marine settings with water depths <50 m.

Included species: *Protopterus humei* (Priem, 1914; sensu Martin, 1984).

Referred Material: CNRST-SUNY 191^{8}, 192^{8}, 193^{8}, 272c^{20}, 273b^{20}, 274c^{20}, 412^{17}, 450d^{7}, 454^{19}, 455^{19}, 456^{19}, and 457^{19}.

Description: New specimens of *Lavocatodus giganteus* documented here include both upper and lower dentitions. Upper dentitions comprise isolated tooth plates (detached from previously supporting pterygoid jaw elements), isolated pterygoids (detached from the tooth plates they supported), and fully articulated pterygoid-tooth plates. Lower dentitions comprise only isolated tooth plates, and these are not associated with prearticular jaw elements. The buccolingual width of upper tooth plates is slightly greater than that of lower tooth plates. Lower tooth plates are almost rectangular, rather than triangular, with the long side directed labially.

For the isolated upper and lower tooth plates collected, the basal surface of each is marked by numerous nutrient grooves that align with the four occlusal ridges. There is wear and some pitting on the occlusal surfaces of most tooth plate specimens, but the occlusal ridges are still well defined. The four occlusal ridges fan out buccoposteriorly (see fig. 63 for a guide to orientation). The ridges are farthest apart mesially and gradually get closer together toward the distal margin of the tooth plate. The mesialmost ridge is also taller compared to more distal ridges. The fourth ridge does not extend as far as the third and does not reach the apex formed by the medial and lingual (symphyseal) margins of the tooth plate. The lingual margin of the tooth plate in *Lavocatodus giganteus* is linear moving toward the posterior edge plate.

DISCUSSION: Lungfish teeth are distinct elements of the Malian fauna and appear taphonomically resistant as they are often recovered intact from phosphate deposits in which other bones are highly polished or damaged. *Lavocatodus giganteus* was erected as the type species of *Lavocatodus* by Martin (1995) for specimens coming from the Paleocene deposits of In Fargas, Mali. *Lavocatodus* and its species are considered members of Lepidosirenidae, as per the redefined diagnosis of the Lepidosirenidae by Kemp (1998) and further described by Claeson et al. (2014). Extant members of the Lepidosirenidae are located on the continents of Africa (species of *Protopterus*) and South America (*Lepidosiren paradoxa*) and are classified as primarily freshwater fishes due to an observed physiological intolerance of saline water (Myers, 1938). The temporal range of *L. giganteus* was recently extended back approximately 13 million years to the middle Campanian of Egypt by Claeson et al. (2014). The age of the new specimens described here is congruent with the previously noted temporal range extension of the taxon.

Lungfish remains from the Trans-Saharan Seaway demonstrate signature taphonomy that indicates they were originally freshwater and reworked within marine depositions (Martin, 1984). Specifically, there is less wear and polishing than in marine rocks. Dental remains of *Neoceratodus africanus* suggested to be *L. giganteus* by Claeson et al. (2014) are much more frequent in continental than in marine rocks. Another circumstantial variable suggesting that the Malian lungfish lived in freshwater habitats was underscored by Martin (1984) who noted that marine lungfish dentitions tend to be found in association with cranial roof bones, a relationship that is not the case for the Malian material. Malian remains of *Lavocatodus giganteus* are one example of indirect evidence of a vast reach of ancient freshwater systems that spread geographically across what is the present-day Sahara (Otero, 2011). It is noteworthy that, based on the stratigraphic range of specimens we have collected, *Lavocatodus giganteus* appear to have survived the K-Pg boundary in Mali.

Protopterus elongus Martin, 1995

Figures 64, 65

HORIZON IN STUDY AREA AND AGE: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

LOCALITY: Mali-20 unit 2.

DEPOSITIONAL ENVIRONMENT: Phosphate conglomerates (Facies 5); shallow marine-to-brackish water phosphorites.

REFERRED MATERIAL: CNRST-SUNY 248 (right pterygoid with tooth plate), 264 (right prearcticular with tooth plate), 386 (left prearticular with tooth plate), 386b (left prearticular with tooth plate), 388 (right pterygoid with tooth plate), 388b (left prearticular with tooth plate), 388c (left prearticular with tooth plate), 388d (right prearcticular with tooth plate), 389 (left pterygoid with tooth plate).

DESCRIPTION: Collected left and right prearticulars (lower jaws) that appear to vary in size isometrically and may represent a growth series. Medially, there is a short, flat symphyseal surface for articulation with its antimere. The coronoid process is preserved posterodorsally on the prearticular, although it is broken in CNRST-SUNY 254. Elsewhere the surfaces are relatively

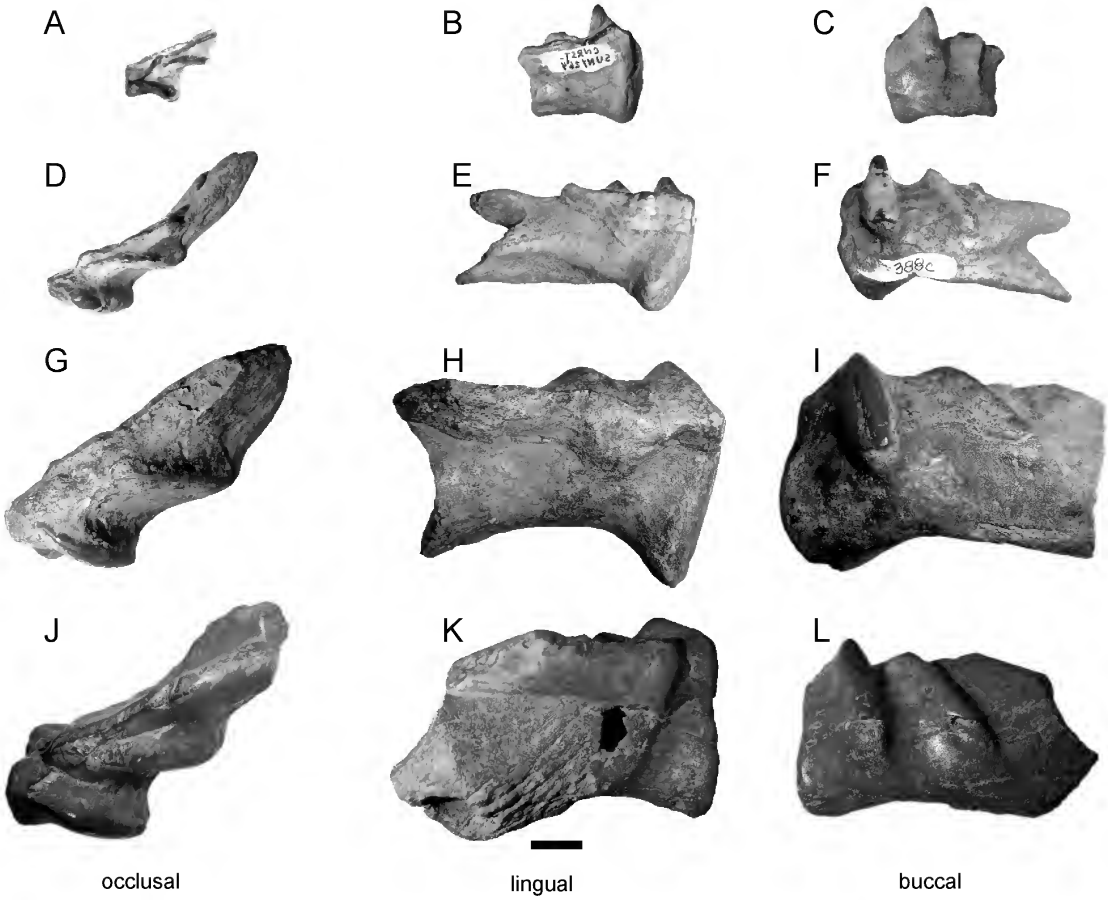


FIGURE 64. Prearticular tooth plates, some with bone, of extinct lungfish *Protopterus elongus* from the Eocene of the Tamaguélelt Formation, Taoudenit Basin, Mali. **A–C,** CNRST-SUNY 264 (right; horizontally flipped in figure); **D–F,** CNRST-SUNY 388c (left); **G–I**, CNRST-SUNY 386 (left); and **J–L,** CNRST-SUNY 254 (right; horizontally flipped in figure). See figure 63 for orientation. Scale bar = 1 cm.

unworn. The articular surface of the tooth plates is relatively flat and parallel with the symphyseal surface of the prearticular, a condition present in modern representatives of Lepidosirenidae (Criswell, 2015). There are three ridges per plate that are tall, narrow, and relatively unworn. There are small cusps on the ridges of CNRST-SUNY 264 and 388. The relative length of each ridge increases from mesial to distal (see fig. 63 for orientation of tooth plate in mouth). Ridges two and three are joined lingually in the largest specimens and are parallel to one another in the smaller specimens. There is a single ridge extending from their merger to the origin of ridge one. Preserved pterygoids and upper tooth plates are larger than the prearticulars and lower tooth plates, thus no two represent directly occluding pairs.

The presence of only three occlusal ridges on tooth plates is a diagnostic characteristic of *Protopterus* (Apesteguía et al., 2007: chars. 9, 10), as are midline-fused right and left prearticulars and a coronoid process on the prearticular (Criswell, 2015: chars. 32 and 25, respectively).

Discussion: The fossil record of *Protopterus* in Africa is extensive throughout the Cenozoic,

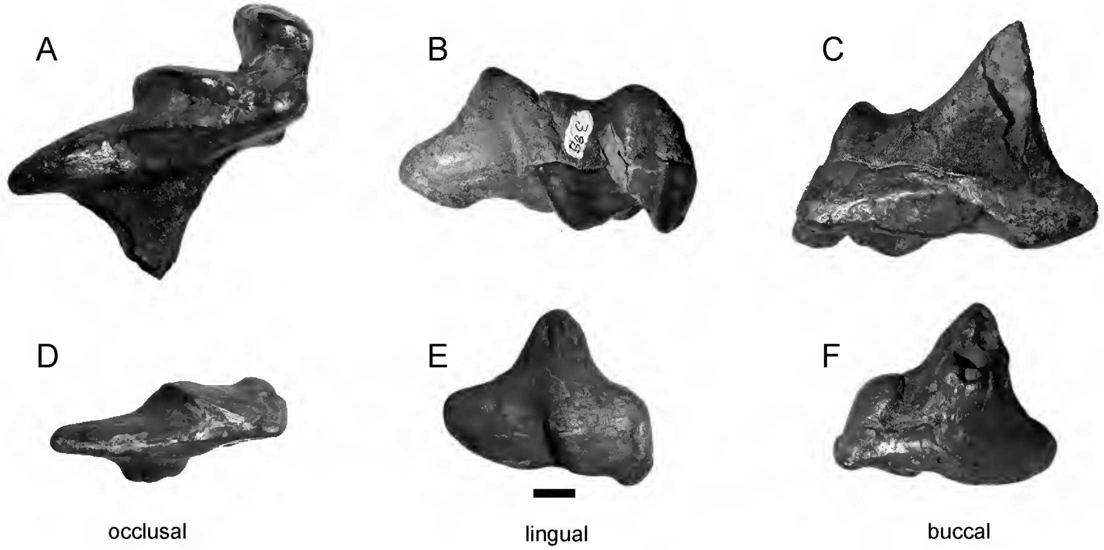


FIGURE 65. Exemplars of the right pterygoid tooth plates and bone of the extinct lungfish *Protopterus elongus* from the Eocene of the Tamaguélelt Formation, Taoudenit Basin, Mali. **A–C,** CNRST-SUNY 388 in **A,** occlusal; **B,** lingual; and **C,** buccal view; **D–F,** CNRST-SUNY 248 in **D,** occlusal; **E,** lingual; and **F,** buccal views. See figure 63 for orientation. Scale bar = 1 cm.

with specimens coming from localities that span a great extent of northern and central Africa (Otero, 2011). *Protopterus* specimens were previously described from the Eocene Tamaguélelt with little information on the particular geology associated with them (Lavocat, 1955). The oldest *Protopterus* specimens are Cenomanian, from the Sudan Wadi Milk Formation and were tentatively assigned to *Protopterus nigeriensis* by Claeson et al. (2014).

The new specimens from Mali are consistent with the type specimen of *Protopterus elongus* in that they exhibit a third ridge that is twice the length of the first ridge. Relative occlusal tooth ridge length in CNRST-SUNY 264 and 388 is similar to lengths described of Egyptian Eocene specimens assigned of *P. elongus* (Murray et al., 2010). New Malian specimens do not represent an extension of Coniacian-Santonian lepidosirenid from Niger *Protopterus nigeriensis* in which the relative length of the third ridge is approximately 1.5 × the size of the first ridge the prearticular tooth plate in the (Martin, 1997). The peaks present on the ridges of tooth plates CNRST-SUNY 264 and 388 are more consistent with cusps like those in the *P. nigeriensis* specimen MUVP 57 (Claeson et al., 2014) and *Protopterus annectens* (Kemp, 2003).

AMNIOTA Haeckel, 1866

SQUAMATA Oppel, 1811

SERPENTES Linnaeus, 1758

PALAEOPHIIDAE Lydekker, 1888

Palaeophis colossaeus Rage, 1983

Figure 66

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Localities: Mali-20 units 2, 4 (Mali-20b, middle phosphates), and 7 (Mali-20c, upper phosphates).

Depositional Environment: Phosphate conglomerates (Facies 5); shallow marine-to-brackish water phosphorites.

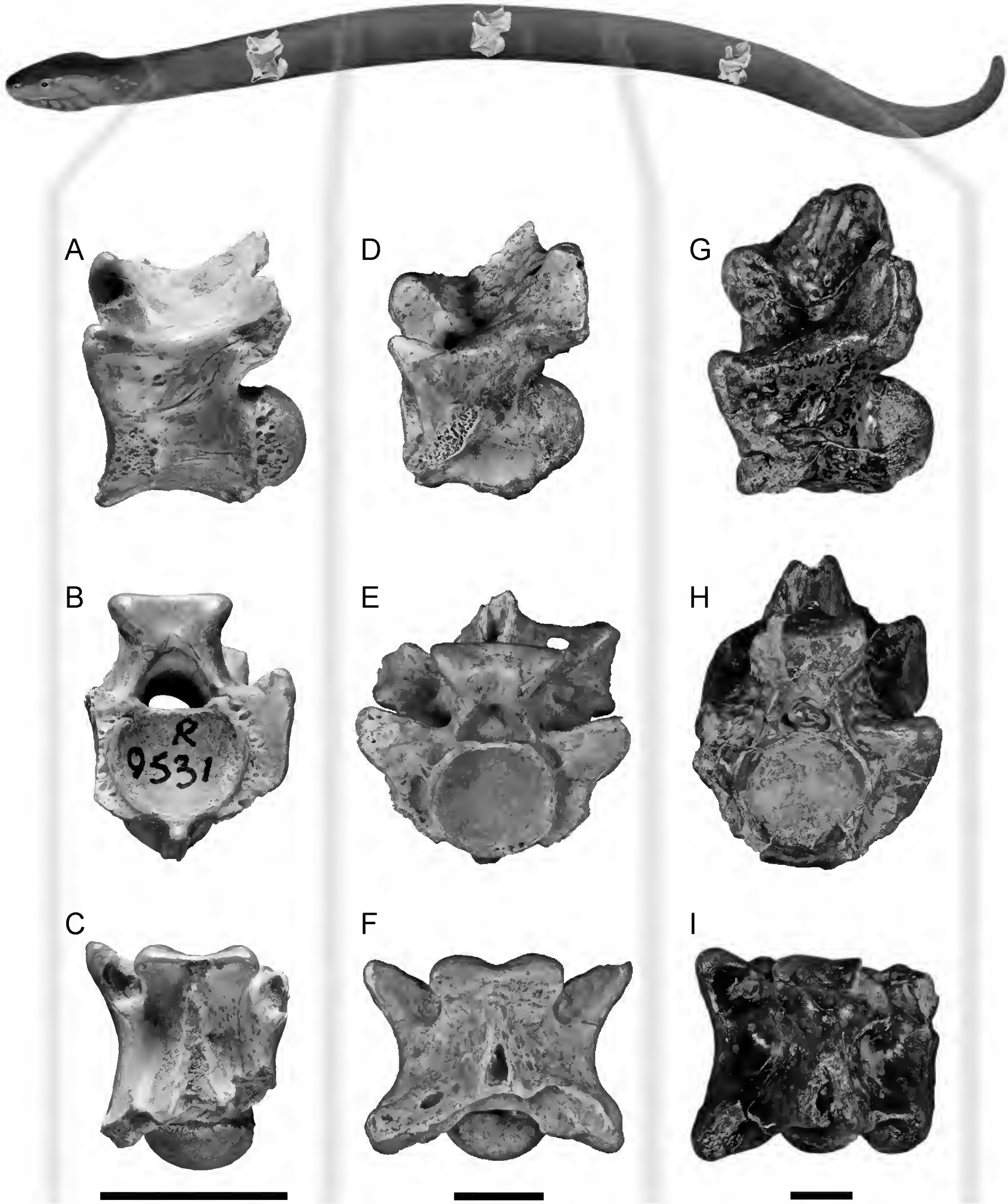


FIGURE 66. Three *Palaeophis colossaeus* specimens from the upper phosphates of Mali-20, Eocene of the Tamaguélelt Formation, Taoudenit Basin. **A–C,** anterior trunk vertebra (NHMUK PV R 9531) in **A,** lateral; **B,** anterior; and **C,** dorsal views; **D–F,** midtrunk vertebra (CNRST-SUNY 310) in **D,** lateral; **E,** anterior; and **F,** dorsal views; and **G–I,** posterior trunk vertebra (CNRST-SUNY 293) in **G,** lateral; **H,** anterior; and **I,** dorsal views. The reconstruction along the top demonstrates the general region in the column for each vertebra. Scale bar = 1 cm.

Referred Material: CNRST-SUNY 306$^{20\text{ unit }2}$, 308, 309$^{20\text{ unit }7}$, 323$^{20\text{ unit }2}$, anterior trunk vertebrae; CNRST-SUNY 297, 299, 300, 301, 313, 316, 321$^{20\text{ unit }2}$, anterior or midtrunk vertebrae; CNRST-SUNY 261$^{20\text{ unit }2}$, 288, 291, 292, 294, 295$^{20\text{ unit }7}$, 304, 305$^{20\text{ unit }2}$, 310$^{20\text{ unit }7}$, 315, 325$^{20\text{ unit }2}$, midtrunk vertebrae; CNRST-SUNY 289$^{20\text{ unit }7}$, 296, 302, 311, 318, 322$^{20\text{ unit }2}$, midtrunk or posterior trunk vertebrae; CNRST-SUNY 293$^{20\text{ unit }7}$, 320$^{20\text{ unit }2}$, posterior trunk vertebrae; CNRST-SUNY 290$^{20\text{ unit }7}$, 298, 303$^{20\text{ unit }2}$, 307$^{20\text{ unit }7}$, 312, 314, 317, 319$^{20\text{ unit }2}$, trunk vertebrae.

Description: Revised diagnosis taken from McCartney et al. (2018). Distinct from all other snakes by the following combination of characters: robust, large vertebrae lacking prezygapophyseal accessory processes and with a parazygosphenal foramen in the mid- and posterior trunk. Differentiated from all other palaeophiids by greater size and the presence of parazygosphenal foramina in the mid- and posterior trunk. Further distinct from *Pterosphenus* and all *Palaeophis* except *Palaeophis maghrebianus* and *Palaeophis virginianus* by lacking any lateral compression in the vertebrae. Separated from *Pa. maghrebianus* by having a greater width of the zygosphene relative to that of the cotyle, and from *Pa. virginianus* by having a neural spine that arises from immediately posterior to the zygosphene.

Discussion: Snakes of the Trans-Saharan Seaway are predominantly species of Palaeophiidae, an enigmatic clade of presumably marine snakes with a pan-Tethyan distribution from the Cenomanian (Rage and Werner, 1999) through the Eocene (Hoffstetter, 1958; Holman, 1977; Averianov, 1997; McCartney and Seiffert, 2016). In the Trans-Saharan Seaway, at least two species are known to occur, both from the Eocene: *Palaeophis africanus* from Niger (Andrews, 1924) and *Palaeophis colossaeus* from Mali (Rage, 1983).

Palaeophiid snakes are considered to be highly adapted to aquatic environments due to their transversely narrow vertebrae and straight, ventrally situated ribs, which produce a narrow, deep body suitable for swimming. Partly due to the hypothesized marine adaptations of these taxa, the placement of this family within crown Serpentes is uncertain. Each species is known from fragmentary material (mainly vertebrae and ribs) and there are no formal phylogenetic analyses incorporating these fossils with living species. One analysis of extinct species that is composed exclusively of vertebral characters does include several species (Averianov, 1997).

The only palaeophiid known from Mali is *Palaeophis colossaeus*, one of the largest known snakes (Rage, 1983; McCartney et al., 2018). Although palaeophiids are generally considered to be aquatic, there is a continuum of morphologies ranging from those that suggest a relatively unspecialized morphology, to those that are highly modified for aquatic life (Rage, 1983; Rage et al., 2003). *Palaeophis colossaeus* is a representative of the former group, with rather broad vertebrae, and ribs that are not set ventrally on the centrum. The presence of these characters has led to the suggestion that *P. colossaeus* represents the basal condition of the family (Rage, 1983), albeit as a late occurring member. However, it should be noted that the body type of snakes in general is particularly suited for swimming, and, among living snakes, even those that show few of the recognized anatomical aquatic adaptations are capable swimmers. *Palaeophis africanus* is often included in the group of palaeophiids that are morphologically unspecialized, but the vertebrae show greater mediolateral compression than in other species of that assemblage, suggesting some specialization for an aquatic lifestyle (Rage et al., 2003).

Estimates of the body size of *Palaeophis colossaeus* have been reported to exceed 9 m (Rage, 1983). Using a regression of cotylar width on body length (detailed in McCartney et al., 2018), the total body length of *P. colossaeus* is estimated to be 12.3 m. Thus *P. colossaeus* was larger than any other known palaeophiid, was the largest known sea snake, and exceeded the size of any living snake species. It is exceeded in size only by the Paleocene boid *Titanoboa* from Colombia (Head et al., 2009). Complicating efforts to estimate its size is the fact that it is known only from isolated vertebrae. In fact, no palaeophiine snake is known from a complete specimen, and very few are known from articulated material at all. The closest possible relative known from a nearly complete skeleton is the small species *Archaeophis proavus* from Monte Bolca in Italy that has more than 500 vertebrae in total (Janensch, 1906), a number that exceeds the vertebral count reported for living snakes (up to 440; Alexander and Gans, 1966). This discrepancy means that any estimates of length for palaeophiids based on comparisons with modern snakes may underestimate the actual size of the snake.

All living snakes are predatory carnivores, and no evidence exists that suggests palaeophiids were any exception. More difficult to determine is whether palaeophiids were macrophagous, that is, had the ability to consume prey of larger diameter than themselves. To settle this question, cranial material is necessary. The closest putative relatives of *Palaeophis* with skulls, *A. proavus* and "*Archaeophis*" *turkmenicus*, provide contradictory evidence as to the kinetic capabilities of the skull. *Archaeophis proavus* has been hypothesized to have had a kinetic skull similar to that of many living snakes (Janensch, 1906), whereas "*A.*" *turkmenicus* is reported to have less mobile cranial joints. If the skull of *P. colossaeus* was closer to that of *A. proavus*, the upper limit for the size of consumable food would have been quite large. Contemporaneous species that could have been part of the diet of a large, macrophagous snake include sharks, lungfish, pycnodonts and other large fishes, dyrosaurid crocodyliforms (Brochu et al., 2002; Jouve, 2007; Hill et al., 2008; Claeson et al., 2010), and turtles (Gaffney et al., 2007). It is also not certain whether palaeophiids were constrictors. If palaeophiids were macrophagous, it is likely they would have killed large prey before attempting to consume them to prevent serious damage to their heads in the process.

NIGEROPHIIDAE Rage, 1975

Amananulam sanogoi McCartney et al., 2018

Figure 67A–C

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-19 unit 2.

Holotype: CNRST-SUNY 462, a trunk vertebra.

Depositional Environment: Phosphate conglomerates (Facies 5); shallow marine-to-brackish water phosphorites.

Diagnosis: From McCartney et al. (2018). Nigerophiid snake with the autapomorphic restriction of the hemal keel to the posterior quarter of the centrum. Additionally, differentiated from other nigerophiid snakes by the combination of a dorsoventrally tall zygosphene, a dorsally concave neural arch, and a neural spine that is restricted to the posterior one-third of the neural arch.

Discussion: Nigerophiid snakes share certain morphological characteristics with palaeophiids, namely transversely compressed vertebrae and ventrally situated synapophyses. Some authors have considered them closely related (e.g., Rage, 1975), although it is possible that the similarities between both families are a result of convergence due to their shared aquatic habits rather than close relationship. Nigerophiids have also been morphologically linked to extant caenophidian acrochordids (Rage, 1978), which are themselves aquatic snakes. Definitive nigerophiid snakes have distinctive vertebrae, with neural spines restricted to the posterior portion of the neural arch, hemal keels that project strongly ventrally at the posterior portion of the centrum, and weak or absent interzygapophyseal and subcentral ridges. Some species referred to the family lack one or more of these features. Nigerophiids have a similar temporal and geographic distribution as palaeophiids, known from across the Tethys and associated waterways from the Late Cretaceous (Rage and Werner, 1999) through the Eocene (Rage, 1980). Two species of nigerophiid snakes are known

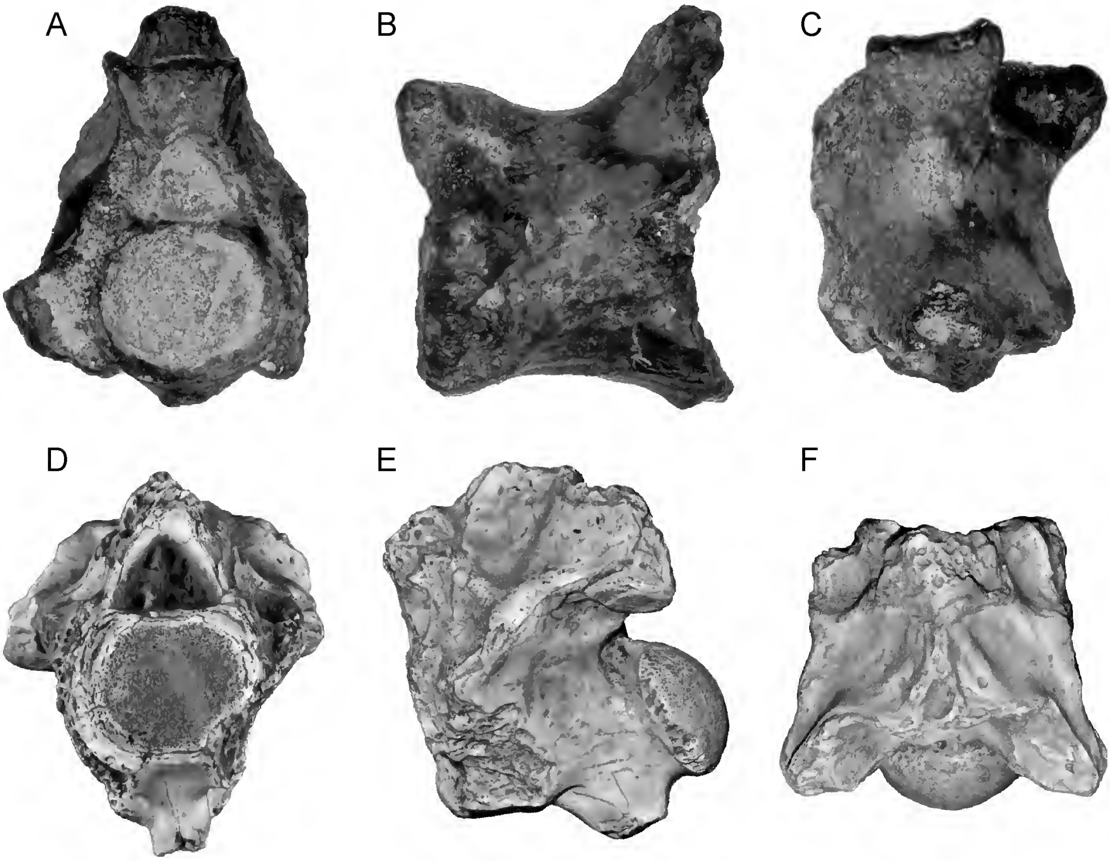


FIGURE 67. Two snake species from the Paleogene of Mali. **A–C,** *Amananulam sanogoi* (CNRST-SUNY 462) from the Paleocene of the Teberemt Formation, Gao Trench in **A,** anterior; **B,** right lateral; and **C,** dorsal views (note that B has been digitally flipped horizontally to facilitate comparison) and **D–F,** Serpentes indet. (CNRST-SUNY 324) from the Eocene of the Tamaguélelt Formation, Taoudenit Basin, Mali in **D,** anterior; **E,** left lateral; and **F,** dorsal views. Scale bar = 1 cm.

from the Trans-Saharan Seaway: *Nigerophis mirus* from the Paleocene of Niger (Rage, 1975), and *Amananulam sanogoi* from the Eocene of Mali (McCartney et al., 2018).

We provide some approximate estimates of body size in these extinct snakes, noting that these estimates are highly preliminary because these fossils are known only from vertebrae. Moreover, there is no cranial material identified for Nigerophiidae, and it is unclear what the closest relative is for comparisons. However, using a regression of cotylar width on body length (detailed in McCartney et al., 2018), we estimate that the total length of the nigerophiid *Amananulam sanogoi* at ~210 cm, much smaller than the estimated body lengths for *Palaeophis colossaeus*. However, among nigerophiids, this size estimate is exceeded only by the estimate for *Nessovophis zhylga*, for which Averianov (1997) reported a cotylar width that suggested a size of 310 cm. We estimate that this clade averaged ~120 cm in length and had species that may have been as short as ~26 cm (again, based on the regression in McCartney et al. [2018] and references therein), thus the Malian species would have been a relatively large nigerophiid. Whether nigerophiids were macrophagous or not, they would have been restricted to consuming relatively small fish or invertebrates.

SERPENTES indet.

Figure 67D–F

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20 unit 2 (Mali-20a, lower phosphates of McCartney et al., 2018).

Depositional Environment: Phosphate conglomerates (Facies 5); shallow marine-to-brackish water phosphoritess.

Referred Material: CNRST-SUNY 324$^{20\ \mathrm{unit}\ 2}$, possible anterior trunk vertebra.

Description: A third snake is represented by a single eroded vertebra probably pertaining to the anterior trunk. All that is preserved is the vertebral centrum and a portion of the neural arch. What is preserved of the zygantrum suggests a moderately thick zygosphene. The cotyle and condyle are nearly circular, and the condyle is turned upward. The subcentral ridges are robust, and converge posteriorly. There is a thick, though incomplete, hypapophysis; a notable gap lies between the base of this process and the condyle.

Discussion: The poor preservation prevents specific identification of the material, but what is preserved eliminates Palaeophiidae and Nigerophiidae as possibilities. The upturned condyle and gap between the hypapophysis and condyle are not found in either clade, and the substantial hypapophysis further separates it from Nigerophiidae. The vertebra is rather robust like many boid-grade snakes, but this robusticity may simply be a result of the relatively large size of the specimen.

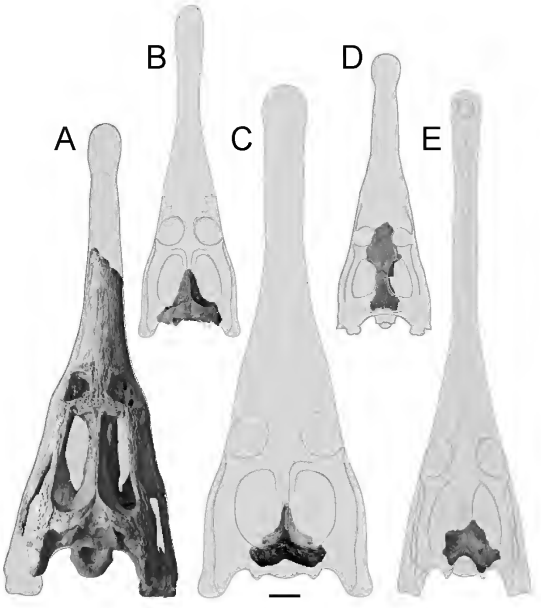


FIGURE 68. Comparison of dyrosaurid braincases from Mali. **A,** *Rhabdognathus aslerensis* (CNRST-SUNY 190) from the K-Pg boundary of the Taoudenit Basin; **B,** Hyposaurinae indet. (CNRST-SUNY 278) and **C,** cf. *Sokotosuchus*, (CNRST-SUNY 279), from the Paleocene of the Teberemt Formation, Gao Trench; **D,** *Chenanisuchus lateroculi* (CNRST-SUNY 280) and **E,** *Rhabdognathus keiniensis* (CNRST-SUNY 277). from the Maastrichtian of the Ménaka Formation, Gao Trench. Scale bar = 2 cm.

CROCODYLIFORMES Hay, 1930, sensu Benton and Clark, 1988

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

DYROSAURIDAE de Stefano, 1903

Chenanisuchus Jouve et al., 2005a

Chenanisuchus lateroculi Jouve et al., 2005a

Figures 68, 69A

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-8 unit 10.

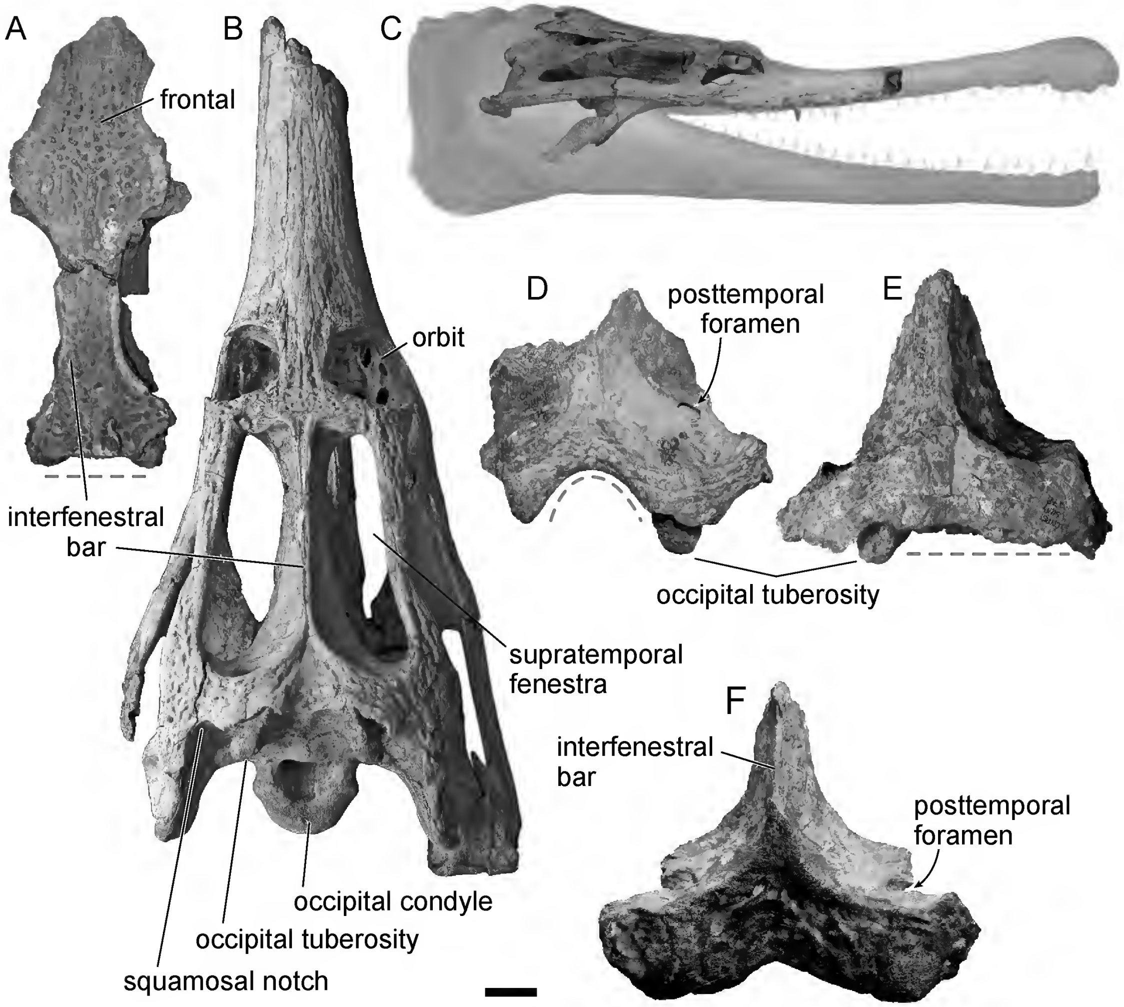


FIGURE 69. Dyrosaurid braincases from Mali, fossils and reconstruction. **A,** *Chenanisuchus lateroculi* (CNRST-SUNY 280); **B–C,** *Rhabdognathus aslerensis* (CNRST-SUNY 190), **B,** dorsal view of specimen and **C,** lateral view with life reconstruction; **D,** *Rhabdognathus keiniensis* (CNRST-SUNY 277) in dorsal view; **E,** Hyposaurinae indet. (CNRST-SUNY 278) in dorsal view; and **F,** Phosphatosaurinae cf. *Sokotosuchus* (CNRST-SUNY 279) in dorsal view. Locality information given in figure 68. Red dotted lines emphasize differences in the caudal margin of the skull roof between species. Scale bar = 1 cm.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 280; partial skull roof and occiput.

Description: The specimen pertains to a dyrosaurid, based on the presence of elongate supratemporal fenestrae and otic capsules that are closely apposed to one another medially. There is a wide interfenestral bar that is T-shaped in cross section, a character that is autapomorphic for *Chenanisuchus* (Jouve et al., 2005a).

Discussion: Due to its short snout and other characters that are atypical of Dyrosauridae, *Chenanisuchus* is not easily allied with other dyrosaurid genera. Phylogenetic analyses have tended to place this taxon at the base of the dyrosaurid radiation, basal to the divergence of Hyposaurinae from Phosphatosaurinae (Jouve et al., 2005b; Barbosa et al., 2008; Hastings et al., 2015). The holotype and a referred specimen are known from Paleocene rocks in Morocco. The discovery of *Chenanisuchus* in Maastrichtian rocks at Mali-8 demonstrates that this taxon appears to have survived the K-Pg event. This finding also increases the congruence between clade position and age for this taxon: *Chenanisuchus* has a relatively ancient stratigraphic range relative to other dyrosaurids, and a basal phylogenetic position within the dyrosaurid radiation (Hill et al., 2008).

HYPOSAURINAE Buffetaut, 1980

Rhabdognathus Swinton, 1930

Rhabdognathus aslerensis Jouve, 2007

Figures 68, 69B, C

Horizon in Study Area and Age: Base of Teberemt Formation and base of the regionally extensive "Terrecht I" limestone unit. Taoudenit Basin. Maastrichtian–early-middle Paleocene (late Danian-Selandian?).

Locality: Mali-5, near the village of Asler.

Holotype: CNRST-SUNY 190.

Depositional Environment: Pale yellow, sandy limestone; shallow marine (Facies 3), interpreted as having formed in shallow, sublittoral conditions under normal marine salinity.

Description: This specimen represents the most complete dyrosaurid fossil from the Mali localities. It is a well-preserved and relatively undistorted skull, missing only the left quadrate and the rostralmost tip of the snout. Brochu et al. (2002) provided a complete description of the specimen.

Discussion: Swinton (1930) erected the genus *Rhabdognathus* and its type species, *R. rarus*, on the basis of a mandibular fragment from the Paleocene of Nigeria. Despite the absence of anatomically overlapping characters, Buffetaut (1980) referred a nearly complete skull (MNHN TGE 4031) to this genus and species. Brochu et al. (2002) declined to refer CNRST-SUNY 190 to *R. rarus*, instead referring it tentatively to cf. *Rhabdognathus* sp. based on morphology of the supratemporal fenestrae, which bear similarities to other specimens referred to various species of *Rhabdognathus*. Jouve (2007) synthesized over seven decades of research on this genus in a comprehensive review of the dyrosaurid material from the Paleocene of the Iullemmeden Basin. Because no cranial material could be referred confidently to the type species, *R. rarus*, he divided *Rhabdognathus* into two species, designating CNRST-SUNY 190 as the holotype of *R. aslerensis*. Diagnostic characters of *R. aslerensis* include a wide, V-shaped basioccipital in occipital view and a moderately exposed posterior wall of the supratemporal fenestra in dorsal view. Additionally, the posterior margin of the parietal is only gently concave in dorsal view, unlike the deep concavity of *R. keiniensis*. The paroccipital process is long and sharp, and much longer than the occipital tuberosity (Jouve, 2007).

Rhabdognathus keiniensis Jouve, 2007

Figures 68, 69D

Horizon in Study Area and Age: Ménaka Formation of the Iullemmeden Basin. Maastrichtian.

Locality: Mali-8 unit 10.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 276 and 277; each a partial caudal skull roof and occiput (Hill et al., 2008).

Description: CNRST-SUNY 276 and 277 preserve almost identical portions of the skull roof and occiput. As described for the holotype by Jouve (2007), the occipital tuberosities are well developed and sharp, with a deep concavity between them. The concavity manifests both as a depression in the occipital surface and an emargination of the caudal border of the skull roof in dorsal view. The concavity reaches the

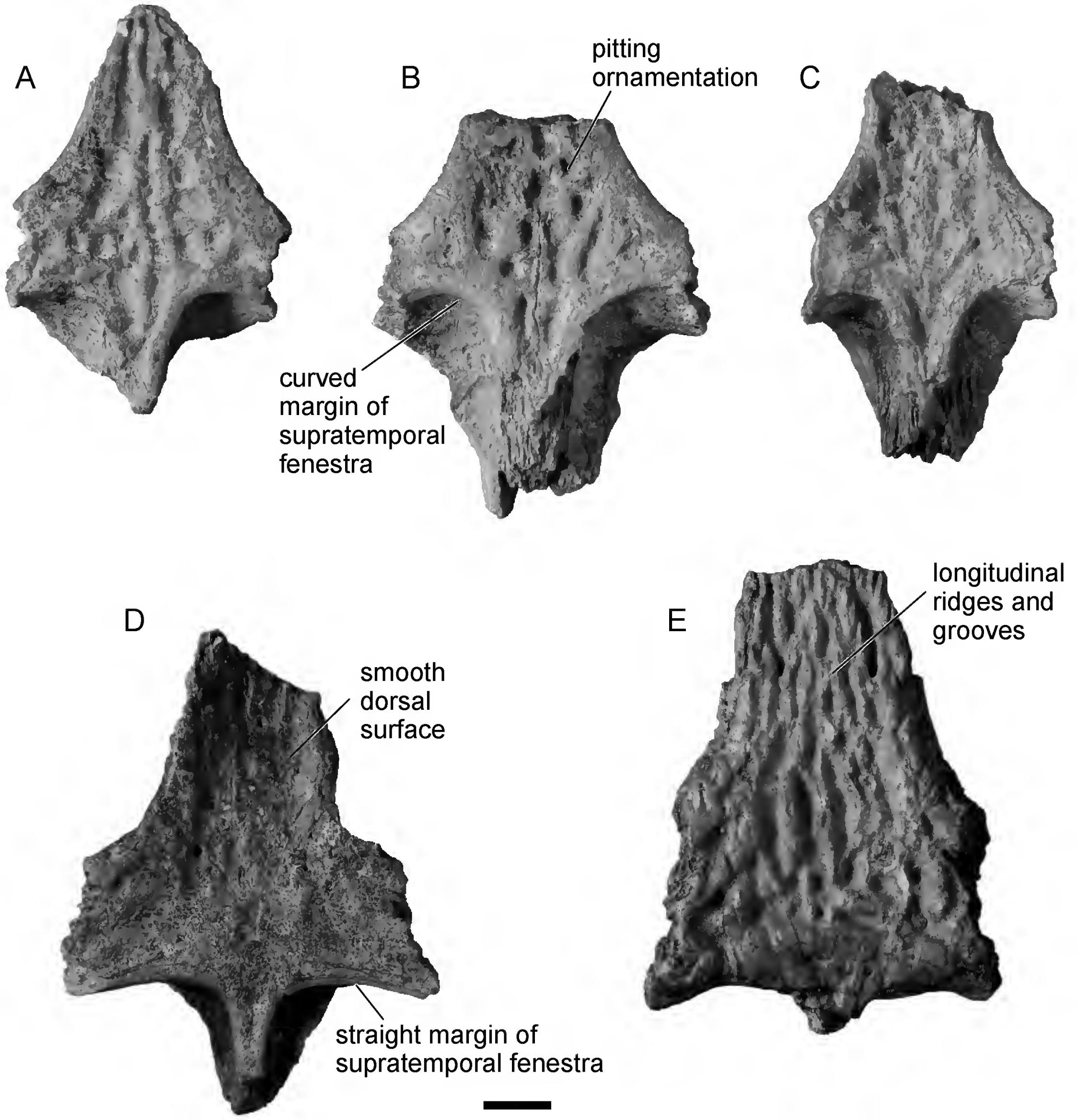


FIGURE 70. Isolated frontal bones of Hyposaurinae indet. (CNRST-SUNY 377) from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. **A–C,** morphotype consistent with prior descriptions of *Hyposaurus*; **D,** a second morphotype, consistent with prior descriptions of *Rhabdognathus*; and **E,** a third morphotype. Scale bar = 1 cm.

level of the caudal margin of the supratemporal fenestra in CNRST-SUNY 277, and nearly reaches it in CNRST-SUNY 276. An additional concavity in the caudal squamosal margin, lateral to the occipital tuberosities, is present in both specimens.

Discussion: Although fragmentary, the referred material preserves the long occipital tuberosities and deep, semicircular emargination of the caudal margin of the skull roof autapomorphic of *R. keiniensis*. Jouve (2007) erected this taxon when revising *R. rarus*, which he

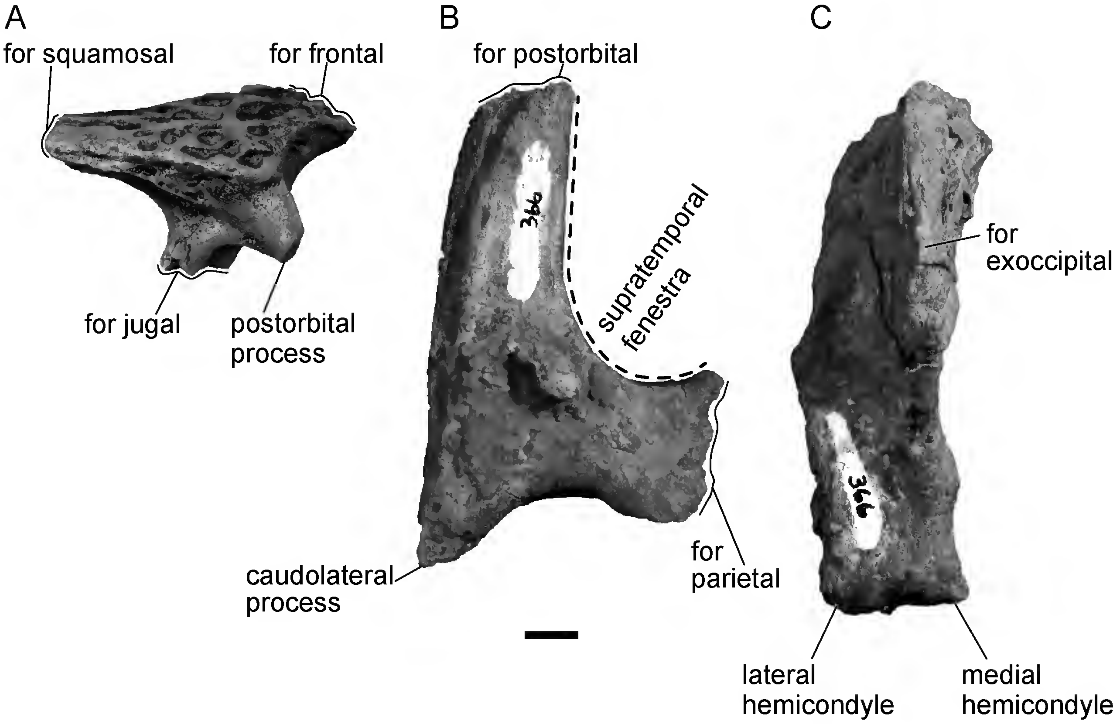


FIGURE 71. Hyposaurinae indet., isolated cranial elements (CNRST-SUNY 366) from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. **A,** right postorbital in lateral view; **B,** ?left squamosal in dorsal view; **C,** left quadrate in caudodorsal view. Scale bar = 1 cm.

deemed a nomen dubium because it was based on a mandibular fragment that is informative only at the generic level. The discovery of *Rhabdognathus* at a Maastrichtian locality indicates the presence of this lineage on both sides of the K-Pg boundary, and the survivorship of this clade across this extinction event.

HYPOSAURINAE Buffetaut, 1980

gen. et sp. indet.

Figures 68, 69E, 70–75

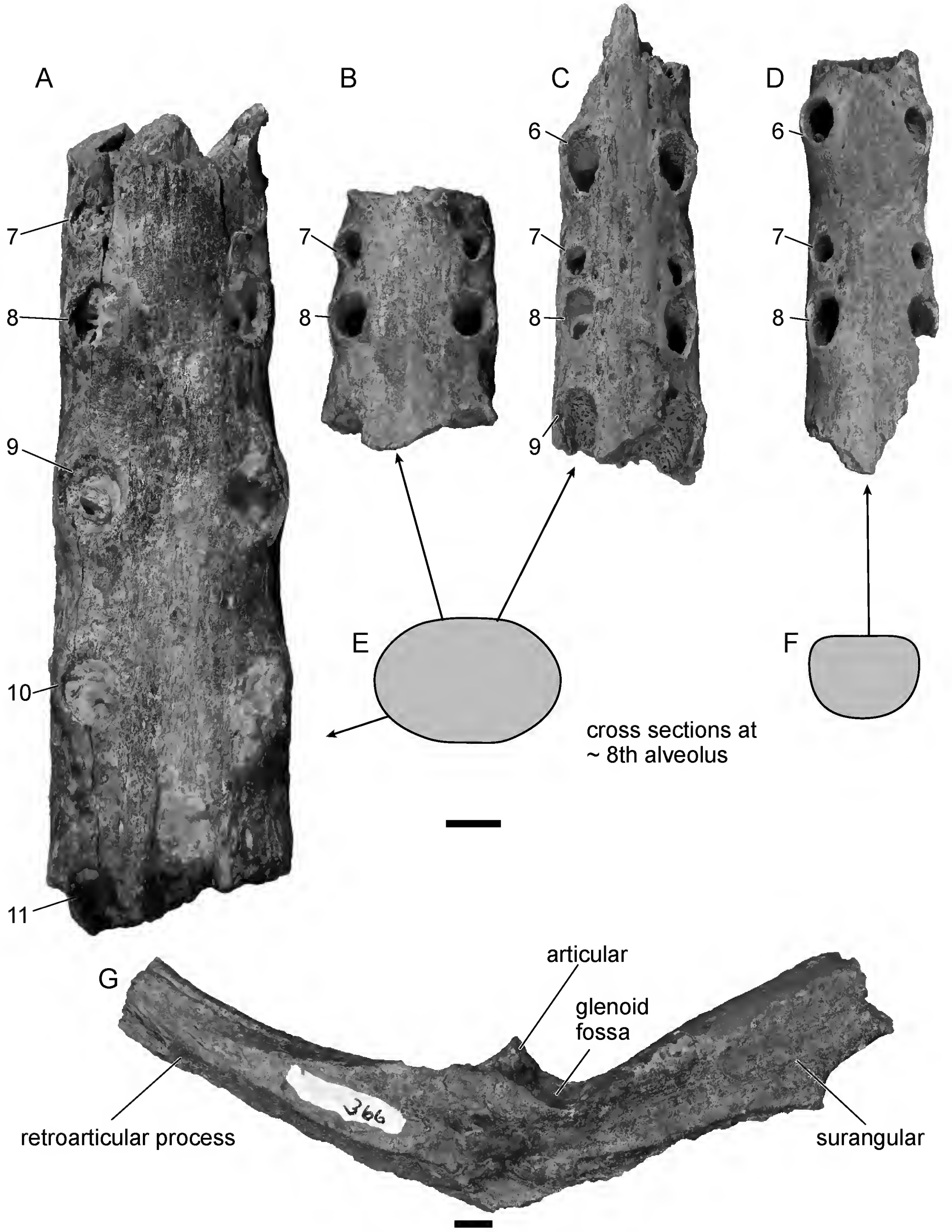
Horizons in Study Area and Age: Ménaka Formation of the Iullemmeden Basin and Teberemt Formation of the Gao Trench. Maastrichtian through Paleocene.

Localities: Mali-8 unit 10 and Mali-18 unit 2.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY $278^{18\ \mathrm{unit\ 2}}$, partial braincase and occipital region of cranium; 284^{8}, partial scapula; 357^{8} and 358^{8}, fragmentary humeri; 360^{8}, a proximal femur; 361, a proximal tibia; 363^{8}, numerous isolated fragmentary osteoderms; 364^{8}, a caudal vertebral centrum; 365^{8}, two fused sacral vertebrae; 366^{8} and $792–808^{8}$ isolated craniomandibular elements including a postorbital, squamosal, quadrate, and partial mandible; 369^{8}, cervical vertebrae and cervical ribs; 377^{8}, isolated frontal bones; 381, numerous isolated mandibular segments preserving various alveoli; and 400^{18}, an isolated dorsal vertebra.

Description: In addition to more precisely diagnosable species of dyrosaurids, we recovered numerous and varied isolated skeletal elements. We refer these here to Hyposaurinae based on size and similar morphology to previously described hyposaurine dyrosaurids (e.g., Langston, 1995).


A
B
C
D
7
8
9
10
11
7
8
6
7
8
9
6
7
8
E
F
cross sections at
~ 8th alveolus
G
articular
glenoid
fossa
retroarticular process
surangular
366

The partial braincase (CNRST-SUNY 278) is similar in size and overall morphology to specimens of *Rhabdognathus*, but lacks the diagnostic features that would permit assignment to this genus. The isolated frontal bones exhibit at least two morphotypes, distinguishable mainly on the basis of ornamentation and the shape of the orbital and supratemporal margins (fig. 69E). Specimens of the first type possess gently concave orbital margins and deeply curved rostral margins of the supratemporal fenestrae. These specimens are ornamented with deep, subcircular pits and strongly resemble the frontals of *Hyposaurus* figured by Langston (1995; fig. F5). The second morphotype is smooth and unornamented, despite being of similar size. It possesses sharply angular contributions to both the orbit and supratemporal fenestra. Another frontal possesses a combination of these characters, with straight orbital and supratemporal margins, and ornamentation consisting of longitudinal ridges and grooves. Additional cranial elements include a postorbital, squamosal, and quadrate. None of these cranial elements is diagnostic at the generic or specific level.

Fragmentary mandibular remains recovered at locality Mali-8 include numerous dentary segments preserving alveoli but no teeth (fig. 72). The seventh alveolus of Dyrosauridae is diagnostically small, aiding identification of homologous portions of isolated fragments. Like the frontal bones, these dentary segments appear to conform to two morphotypes. The first type is a dorsoventrally flattened cylinder, elliptical in cross section, similar to that reported for *Hyposaurus* (Langston, 1995; Jouve, 2007). The second type is as tall dorsoventrally as it is wide, with a flattened dorsal surface. This morphology resembles *Rhabdognathus* (Langston, 1995; Jouve, 2007). In addition to these dentary remains there is a set of partial postdentary bones including the right articular and retroarticular process.

Numerous indeterminate vertebrae were recovered, representing all parts of the vertebral column (fig. 73). All these specimens have some breakage of vertebral processes. The full extent of the spinous process and hypapophysis cannot be determined. Nevertheless, the presence of a hypapophysis on the cervical and dorsal vertebrae indicates dyrosaurid affinities for these specimens. Vertebral morphology is consistent with that described for hyposaurine dyrosaurids by Schwarz et al. (2006). No dorsal ribs or hemal arches were recovered.

Appendicular remains include a fragmentary scapula and numerous partial limb bones (fig. 74), again similar to postcranial remains of hyposaurines as described by Schwarz et al. (2006). The numerous fragmentary osteoderms recovered represent elements of the dorsal and gastral shields (fig. 75).

PHOSPHATOSAURINAE Buffetaut, 1979

Phosphatosaurus Bergounioux, 1955

Phosphatosaurus gavialoides Bergounioux, 1955

Figure 76

HORIZON IN STUDY AREA AND AGE: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

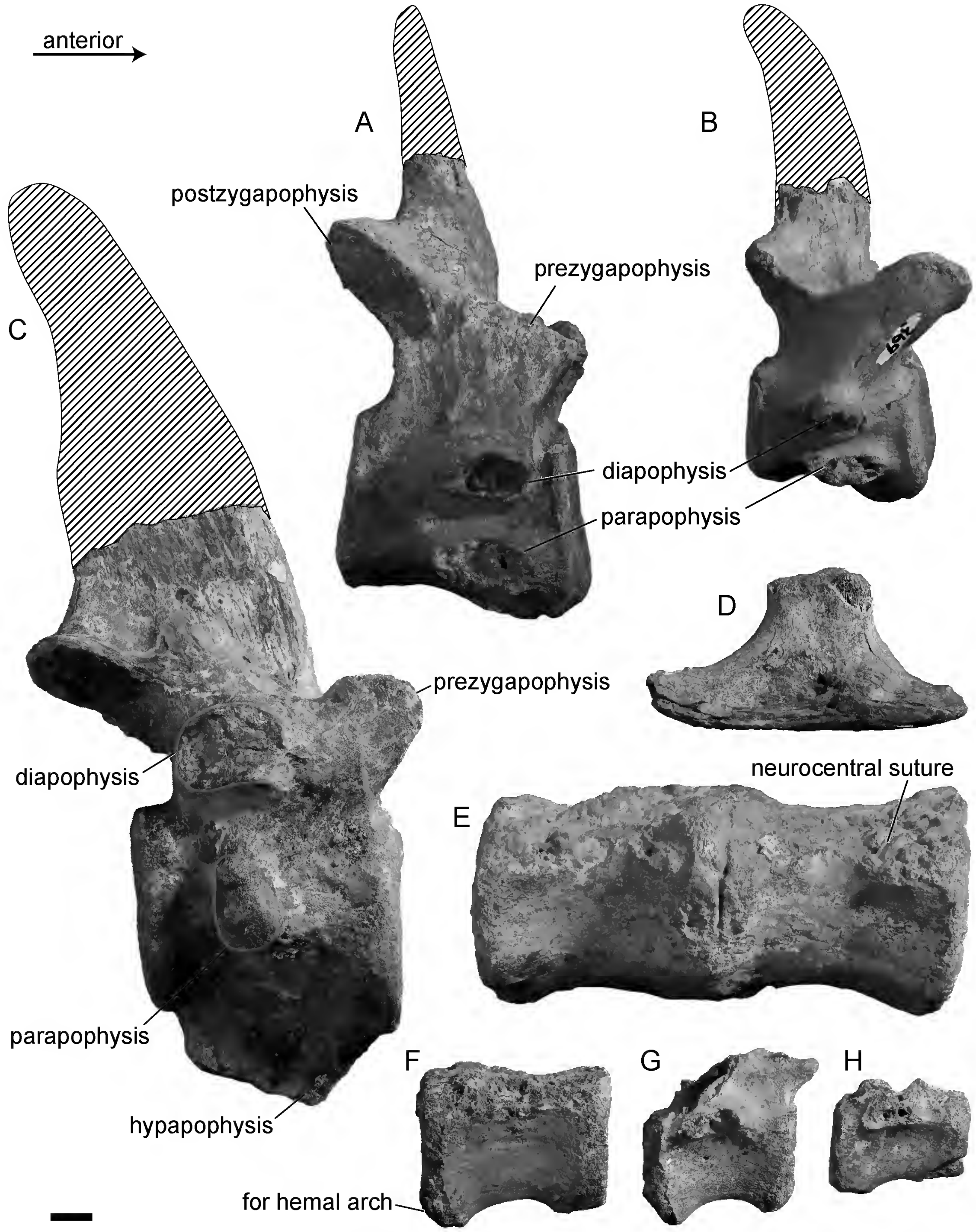
LOCALITY: Mali-20 unit 2 (lower phosphates).

DEPOSITIONAL ENVIRONMENT: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

REFERRED MATERIAL: CNRST-SUNY 275; symphyseal portion of mandible including most of the dentaries and splenials with one replacement tooth (Hill et al., 2008: fig. 4).

◄

FIGURE 72. Hyposaurinae indet., isolated mandibular remains with numbered alveoli from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. **A–D,** partial dentary bones (CNRST-SUNY 381) consistent with prior descriptions of **A–C,** *Hyposaurus* and **D,** *Rhabdognathus.* Cross sections in **E** and **F** show profile at level of eighth alveolus; and **G,** CNRST-SUNY 366, partial set of right postdentary bones in lateral view. Scale bars = 1 cm.


anterior
A
B
C
postzygapophysis
prezygapophysis
diapophysis
parapophysis
D
prezygapophysis
diapophysis
neurocentral suture
E
parapophysis
hypapophysis
F
G
H
for hemal arch

Description: The specimen preserves the left and right dentary bones in articulation, with 10 alveoli on the left side and 12 alveoli on the right. The dentaries are mostly complete to the rostralmost tip of the jaw. A single replacement tooth is embedded in the right fourth alveolus. The rostral portions of both splenials are also preserved, reaching as far rostrally as the ninth alveolus.

Discussion: Bergounioux (1955) diagnosed *Phosphatosaurus gavialoides* as follows: large and massive form, skull subrectangular, symphysis long, rostrum thick, narrowing only gradually from the cranial part, relatively short and terminating in a large spatulate premaxilla that bears three pairs of unequal teeth. Teeth heterodont, rostralmost teeth conical, strong, smooth, with a small apical point; other teeth cylindrical, shorter, with a dorsoventral carina and ornamented with fine longitudinal striations. The referred partial mandible of *P. gavialoides* is more gracile overall than the holotype, but nevertheless shares all diagnostic characters with it.

cf. *Sokotosuchus* Halstead, 1975

Figure 68C, 69F

Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-18 unit 2.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: CNRST-SUNY 279; posterior skull roof and occiput.

Description: This specimen represents the largest-bodied dyrosaurid found at the Mali localities. Although fragmentary, it has the medially contacting otic capsules that are autapomorphic of Dyrosauridae. We tentatively refer it to Phosphatosaurinae based on its large size.

Discussion: Phosphatosaurinae was proposed by Buffetaut (1979) for large-bodied dyrosaurids with a robust skull and a relatively broad snout with large, heterodont teeth, distinct from the slender-snouted, sharp-toothed Hyposaurinae. The referred specimen bears some similarities to the putative phosphatosaurine *Sokotosuchus ianwilsoni* (Halstead, 1975) known previously from the Cretaceous of Nigeria. In the absence of diagnostic characters, however, assignment to this genus is tentative. If the specimen does represent *Sokotosuchus*, its discovery at this Paleocene locality would provide additional evidence of dyrosaurid survivorship across the K-Pg boundary (Hill et al., 2008).

TESTUDINES Linnaeus, 1758

PLEURODIRA Cope, 1864

PELOMEDUSOIDES Cope, 1868

BOTHREMYDIDAE Baur, 1891

TAPHROSPHYINI Gaffney et al., 2006

Acleistochelys Gaffney et al., 2007

Acleistochelys maliensis Gaffney et al., 2007

Figure 77

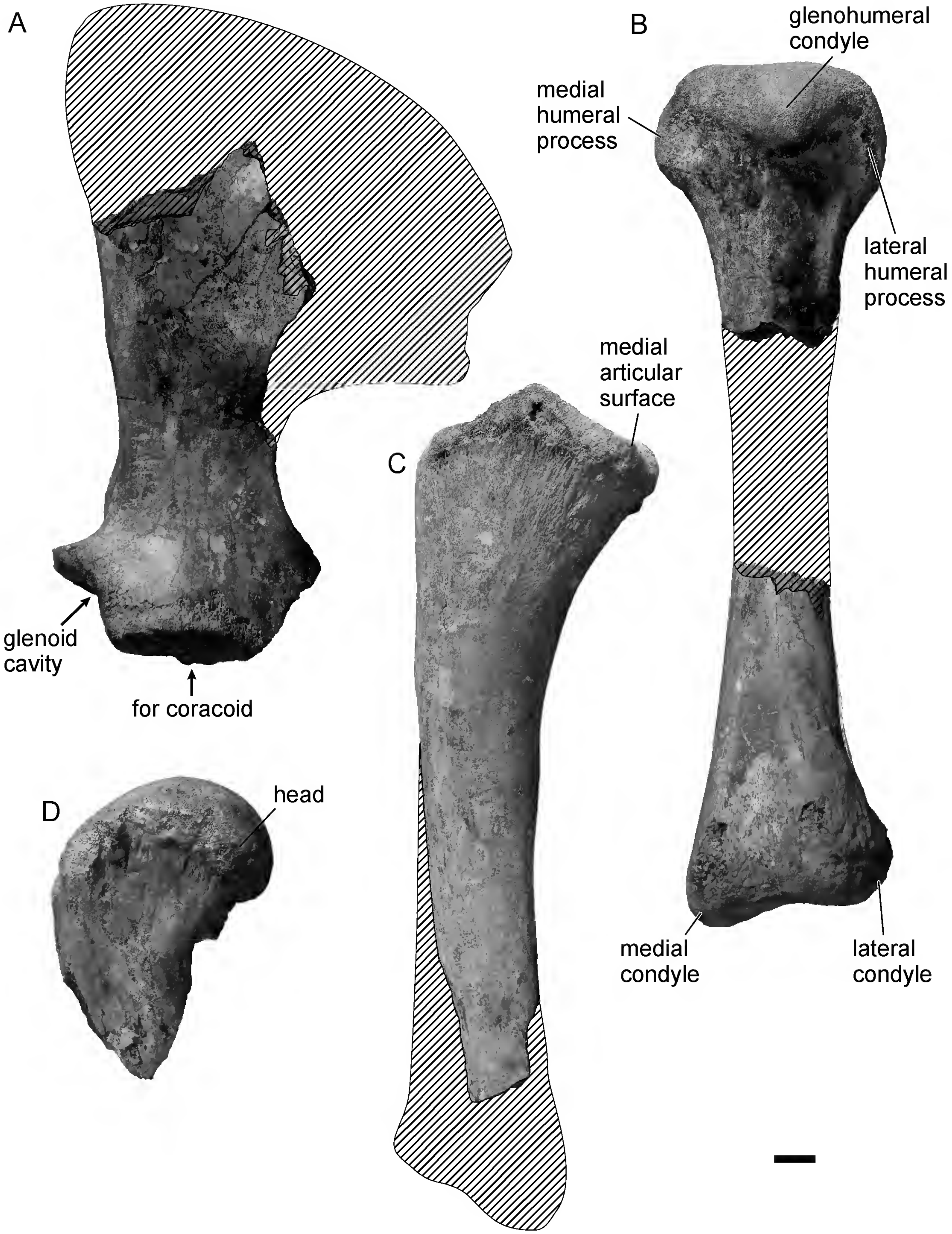
Horizon in Study Area and Age: Teberemt Formation of the Gao Trench. Paleocene.

Locality: Mali-17 unit 3.

Depositional Environment: Interbedded marl and shale (Facies 4); shallow, normal-to-restricted marine deposit.

Holotype: CNRST-SUNY 199.

FIGURE 73. Hyposaurinae indet., isolated elements of axial skeleton. Right lateral views of **A–B,** midcervical vertebrae (CNRST-SUNY 369); **C,** anterior dorsal vertebra (CNRST-SUNY 400); **D,** isolated ?right cervical rib (CNRST-SUNY 369); **E,** two fused sacral vertebral centra (CNRST-SUNY 365); and **F–H,** caudal vertebrae (CNRST-SUNY 364). All specimens from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali, except E, which is from the Paleocene of the Teberemt Formation, Gao Trench. Scale bar = 1 cm.


A
glenoid cavity
for coracoid
B
glenohumeral condyle
medial humeral process
lateral humeral process
medial condyle
lateral condyle
C
medial articular surface
D
head

Referred Material: Nearly complete skull; partial cervical vertebra; pelvic fragments; shell fragments including anterior portion of nuchal, neurals one and four, and peripheral two.

Description: The skull is nearly complete, lacking only a portion of the left temporal region and posterior skull roof. A complete description of the remains was provided by Gaffney et al. (2007).

Discussion: *Acleistochelys* differs from other bothremydid turtles in possessing the following combination of characters: small pit formed between jugal, maxilla, and palatine on triturating surface; wide palatine-basisphenoid contact separating pterygoids on midline; supraoccipital-quadrate contact present; basioccipital narrowly enters occipital condyle; and palatine contact in small septum orbitotemporale (Gaffney et al., 2007). *Acleistochelys* is closely related to another Malian bothremydid, *Azabbaremys moragjonesi*, also from the Paleocene Teberemt Formation (Gaffney et al., 2001; Gaffney et al., 2006). *Acleistochelys* lacks the broad palate and triturating surface of durophagous turtles (Claude et al., 2004) and may have had a piscivorous diet.

PELOMEDUSOIDES Cope, 1868

Gen. et sp. indet.

Figure 78

Horizon in Study Area and Age: Most likely Teberemt Formation of the Gao Trench. Paleocene.

Locality: Noted as near a Samit Camp near In Fargas, 13 km south of Samit, Mali. Collected during the 1981 joint expedition of the British Museum and Kingston Polytechnic Institute.

Referred Material: NHMUK PV R 10917, nearly complete carapace.

Depositional Environment: Limestones, most likely nearshore marine based on comparisons with specimens collected by us, probably our facies 3 or 4.

Description: Large carapace with a craniocaudal length of 0.75 m. Remarkable for possessing an abrupt narrowing at the caudolateral margin of the carapace that results in a lobelike protrusion of the caudal end of the shell in dorsal view. The carapace is nearly complete and articulated. Although a few elements are broken or missing, it largely conforms to the configuration of bones found in other Pelomedusoides, including one nuchal, six or seven neurals, eight pairs of costals, 11 pairs of peripherals, one suprapygal, and one pygal. The nuchal is broken anteriorly, precluding a detailed description of its morphology. The first and second neurals are also missing. The third through sixth neurals are longer than wide and are six-sided, with short anterolateral sides. A seventh, five-sided neural is suggested by a void behind the sixth neural, though the actual bone is not preserved. If present, it was much smaller than the preceding neurals. The first costals are anteroposteriorly longer than the succeeding costals. The seventh and eighth costals are sharply bowed and contact one another on the midline. The suprapygal is broken but appears to have been roughly triangular. The first peripheral is broken and only its caudalmost corner is observed. The second through eighth peripherals are quadrilateral, slightly longer along their outer edges than at their sutures with the costals. The ninth through 11th peripherals are markedly smaller and mediolaterally narrow, coinciding with the pronounced narrowing of the carapace caudally.

Discussion: NHMUK PV R 10917 is a partial shell collected in 1981 by a joint expedition of the Natural History Museum (London) and

FIGURE 74. Hyposaurinae indet., isolated appendicular elements. from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. **A**, fragmentary right scapula (CNRST-SUNY 284) in lateral view; **B**, two possibly associated right humeral fragments (CNRST-SUNY 357 and 358) in posterior view; **C**, partial right tibia (CNRST-SUNY 361) in anterior view; **D**, isolated right femoral head (CNRST-SUNY 360) in anterolateral view. Scale bar = 1 cm.

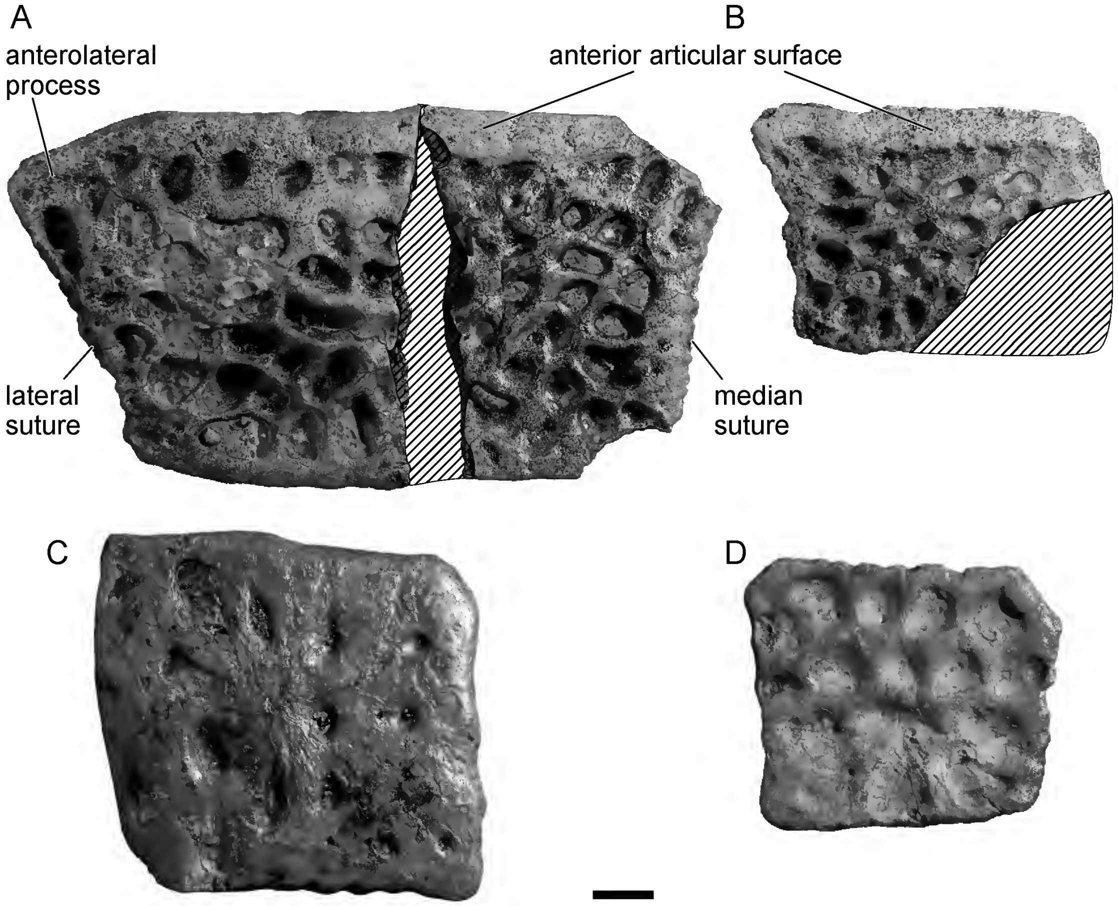


FIGURE 75. Hyposaurinae indet., isolated osteoderms (CNRST-SUNY 363) from the Maastrichtian of the Ménaka Formation, Iullemmeden Basin, Mali. **A–B,** partial dorsal paramedian osteoderms in dorsal view; **C–D,** complete gastral osteoderms in ventral view. Scale bar = 1 cm.

Kingston Polytechnic. Because of its completeness we describe it here. It had been tentatively assigned the taxon "Podocnemid" in museum collection documentation; however, it possesses several features more characteristic of bothremydids. We cannot at this time report on details of the anatomy of the ventral surface of the specimen as full preparation of this large fossil was beyond the scope of this paper.

Shell morphology among Pelomedusoides has been described as highly conservative (Gaffney et al., 2006; 2011). In the absence of associated cranial or other skeletal material, it is difficult to assign this specimen to a more precise taxon than Pelomedusoides. Nevertheless, the specimen appears most similar to members of the tribes Bothremydini and Taphrosphyini figured by Gaffney et al. (2006) and may pertain to one of those taxa. Its occurrence also underscores the tendency of the Samit region localities of the Teberemt Formation to preserve relatively intact bodies of entire organisms. As discussed above, this formation preserved an interesting taphonomic phenomenon of relatively complete turtle shells buried postmortem and encrusted with Ostreida (fig. 11).

MAMMALIA Linnaeus, 1758

PLACENTALIA Owen, 1837;
see also Novacek et al., 1997

PAENUNGULATA Simpson, 1945

HYRACOIDEA Huxley, 1869

PLIOHYRACOIDEA Osborn, 1899

Figure 79A

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

Locality: Mali-20 vicinity.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: NHMUK M 50135, left ?I3.

Description: Isolated tooth with single, robust root and broad, conical, enameled crown terminating in a single cusp. Single crest crosses crown mesiodistally.

Discussion. Specimen was collected by a British expedition and later described by O'Leary et al. (2006). Hyracoids are not typically diagnosed on the morphology of anterior teeth, but close comparisons between this tooth and relatively complete hyracoid specimens revealed similarities with the pliohyracid *Thyrohyrax pygmaeus* (O'Leary et al., 2006). The phosphatic conglomerate at the Tamaguélelt locality that yielded the fossil has a noted preservational bias against mammalian teeth (Tapanila et al., 2008).

TETHYTHERIA McKenna, 1975

PROBOSCIDEA Illiger, 1811

"PLESIELEPHANTIFORMES"
Shoshani et al., 2001

Incertae sedis Sanders et al., 2010

Figures 79B–81

Horizon in Study Area and Age: Tamaguélelt Formation of the Taoudenit Basin. Eocene, possibly lower Eocene.

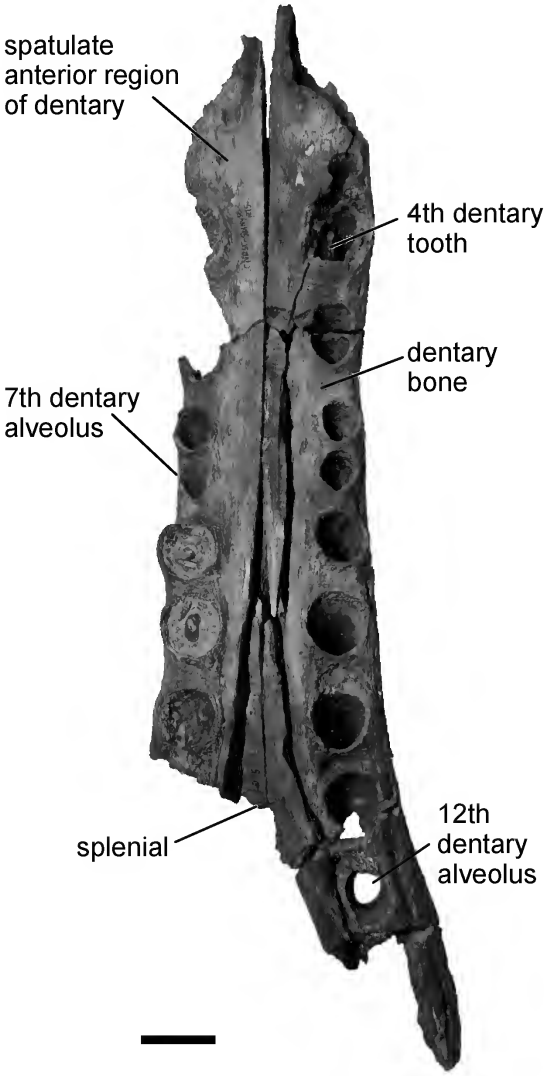


FIGURE 76. *Phosphatosaurus gavialoides* (CNRST-SUNY 275), from the Eocene of the Tamaguélelt Formation, Taoudenit Basin, Mali. Partial mandible in dorsal view. A single replacement tooth is preserved in the right fourth alveolus. Scale bar = 2 cm.

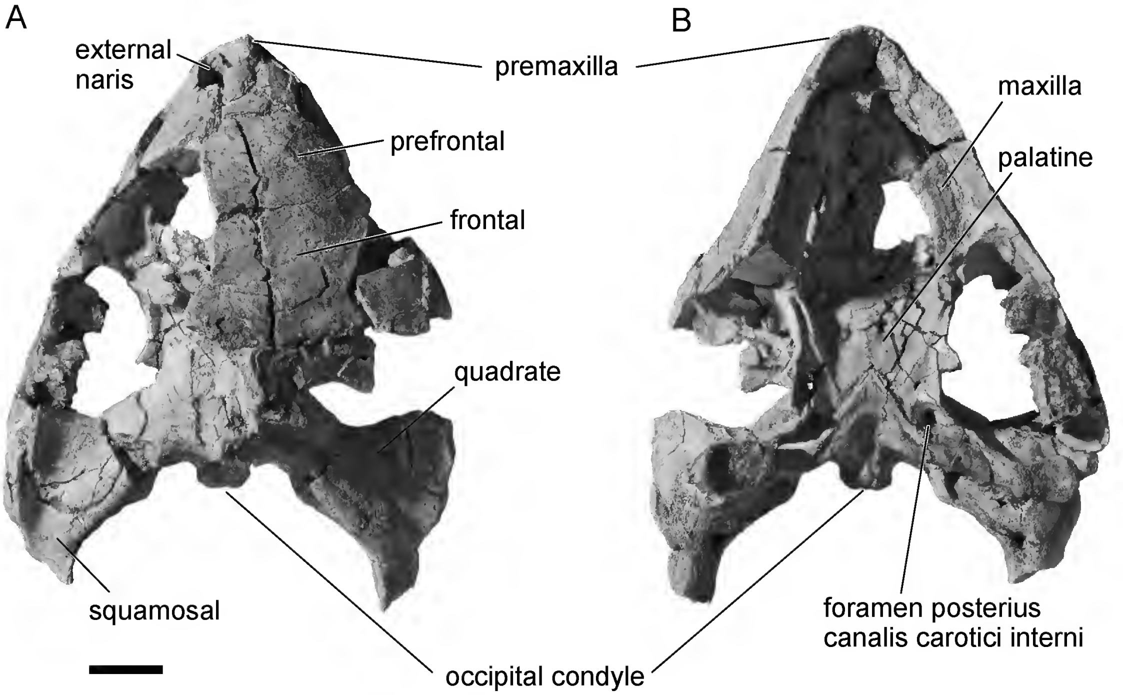


FIGURE 77. *Acleistochelys maliensis* refigured from (Gaffney et al., 2007) from the Paleocene of the Teberemt Formation, Gao Trench. Nearly complete cranium (CNRST-SUNY 199) in **A,** dorsal and **B,** palatal views. Scale bar = 3 cm.

Locality: Mali-20 and vicinity.

Depositional Environment: Phosphatic conglomerate (Facies 5); shallow marine-to-brackish water phosphorites.

Referred Material: Partial right dentary (NHMUK M 51534); partial left dentary (NHMUK M 50129); partial dentaries, sides indeterminate (NHMUK M 50136 and 50137); partial left dentary (NHMUK M 51535); edentulous right maxilla of subadult (CNRST-SUNY 397b); and a fragmentary distal ?ulna (CNRST-SUNY 606), probably from the left side.

Description: O'Leary et al. (2006) described fragmentary gnathic remains of proboscideans from Mali and attributed some of these to Numidotheriidae. Sanders et al. (2010) subsequently revised the higher-level attribution of these specimens to "Plesielephantiformes" incertae sedis with the additional suggestion that the specimens likely represent a new species. We follow that attribution here and provide additional new material.

The best-preserved mandibular specimen (NHMUK M 51534) described in O'Leary et al. (2006), and refigured here, is an edentulous right dentary consisting of the portion between symphysis and ramus. Alveoli correspond to the posterior root of p4, and roots of p5, and m1–m3 using revised placental mammal dental terminology (O'Leary et al., 2013). The alveoli, which are taller labially than lingually, suggest the teeth would have been double rooted. The symphysis has a pronounced lingual inflection.

The newly referred maxilla appears to be that of a subadult individual. The alveolar process of the maxilla in the region over the premolars, and the robust facial process are both preserved. The facial process shows markings of an unfused suture that met either the frontal, nasal, or the premaxilla, as these three bones join in close proximity on the faces of early proboscideans for which more complete skulls are known (Andrews, 1906: fig. 40; Gheerbrant et al., 2005; Sanders et

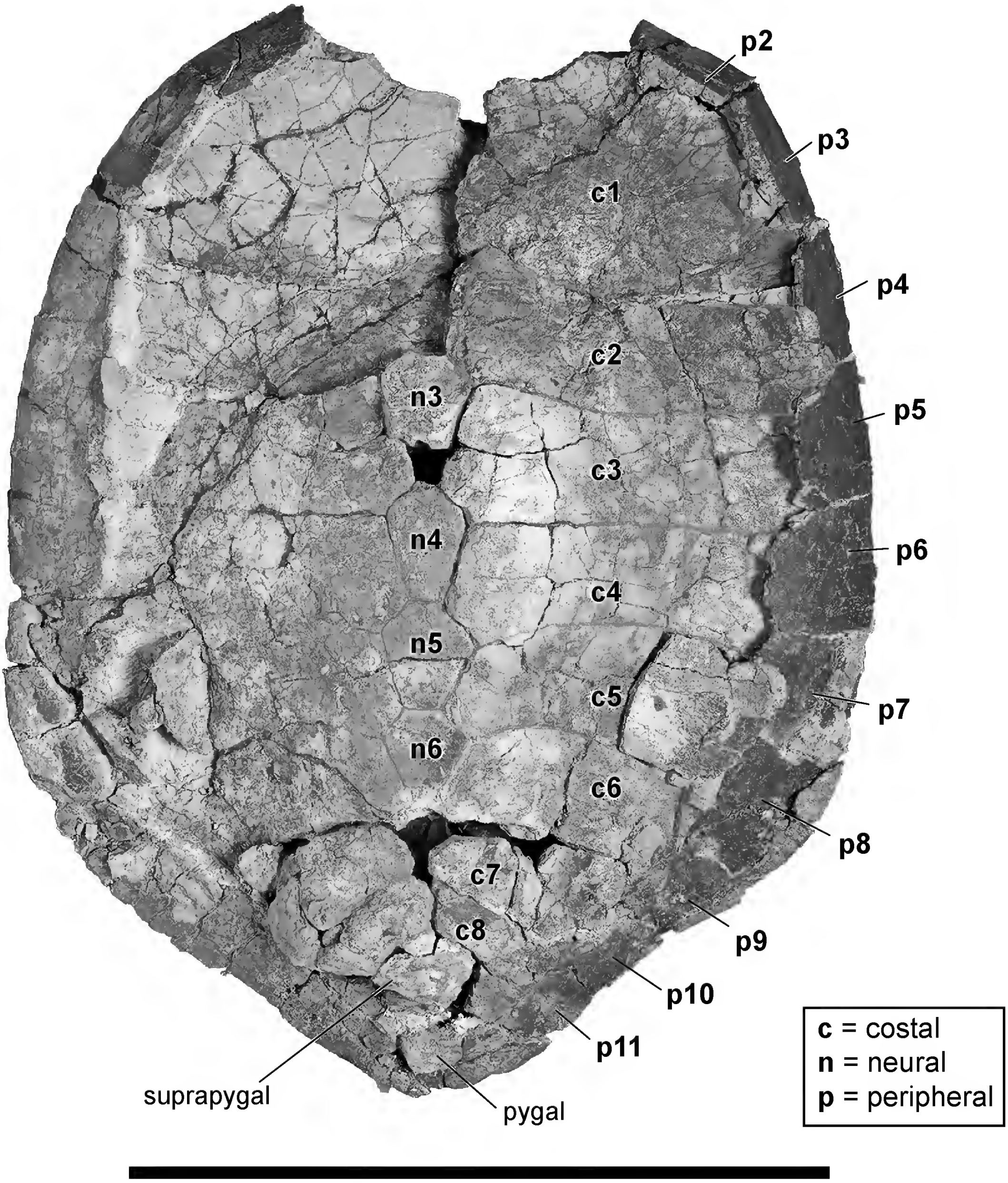


FIGURE 78. Pelomedusoides indet., nearly complete carapace (NHMUK PV R 10917) in dorsal view. Collected by joint expedition of the British Museum and Kingston Polytechnic Institute from the Samit region of the Gao Trench in 1981. Most likely from the Teberemt Formation. Scale bar = 50 cm.

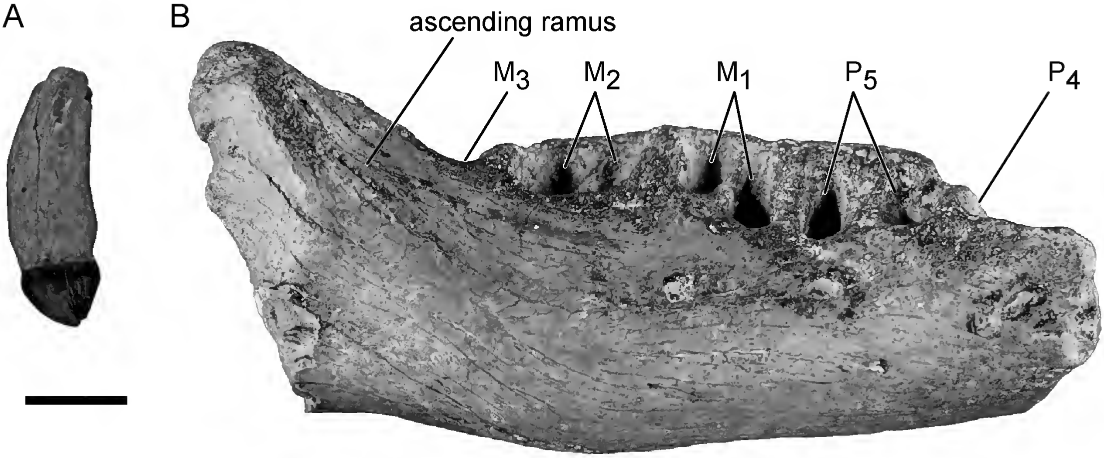


FIGURE 79. Fossil mammals from the Eocene Tamaguélelt Formation, Mali refigured from (O'Leary et al., 2006). **A,** ?left I3 (NHMUK M 50135) of a pliohyracid hyracoid; **B,** edentulous right dentary of a "plesielephantiform" proboscidean (NHMUK M 51534). Scale bar = 1 cm.

al., 2010). Most likely the adjoining bone or bones slid over the maxilla because suture marks are present on the maxilla's lateral surface. Part of the free posterior edge of the maxilla is also intact, which would have formed the root of the zygomatic arch at the anterior border of the infratemporal fossa. The very large posterior opening of the infraorbital canal is well preserved, including multiple, delicate neurovascular channels on the floor of the canal leading into and out of it posteriorly. Lateral to the infraorbital foramen is a robust ridge that lies superior to a gently excavated submaxillary fossa. A single and much smaller anterior foramen that may be continuous with the infraorbital canal is present but broken. Medially, where part of the lateral nasal wall is intact is a ridge that would have constituted the base of a nasal turbinate in life. Superior to this ridge is a pit whose anatomical assessment requires better-preserved material.

The specimen contains two distinct alveoli that are oval in outline with the long axes oriented mediolaterally. These alveoli lie posterior to a large and irregularly shaped but well-preserved tooth crypt that adjoined adjacent alveoli and appears to have contained an unerupted tooth in life. The alveoli appear to have held two sets of compressed roots based on the configuration of the most distal partial alveolus. Some inferences can be made from comparisons with specimens noted below in the Discussion. Using the position of deciduous teeth relative to the posterior opening of the infraorbital canal in specimens where all these structures are preserved, the best-preserved alveolus may represent that of DP5 (note, again, mammalian dental terminology follows O'Leary et al., 2013). The large crypt/alveoli anterior to it may have held DP4 as well as an erupting adult tooth.

We also refer to this taxon a fragmentary bone that appears to be a distal left ulna preserving the distal facet and parts of its extension onto the shaft. The distal articular facet is a craniocaudally elongate, saddle-shaped joint. The anterior aspect of the distal facet is more planar and reaches a gentle point anteriorly. The posterior aspect of the facet is relatively bulbous and wraps onto both the lateral and medial surfaces of the shaft (the lateral surface is better preserved). There is a gentle pit at the base of the shaft on the medial side of the bone. What remains of the shaft suggests it was laterally compressed. One taphonomic observation: the broken bone has a coprolite cemented to it. Coprolites comprise a

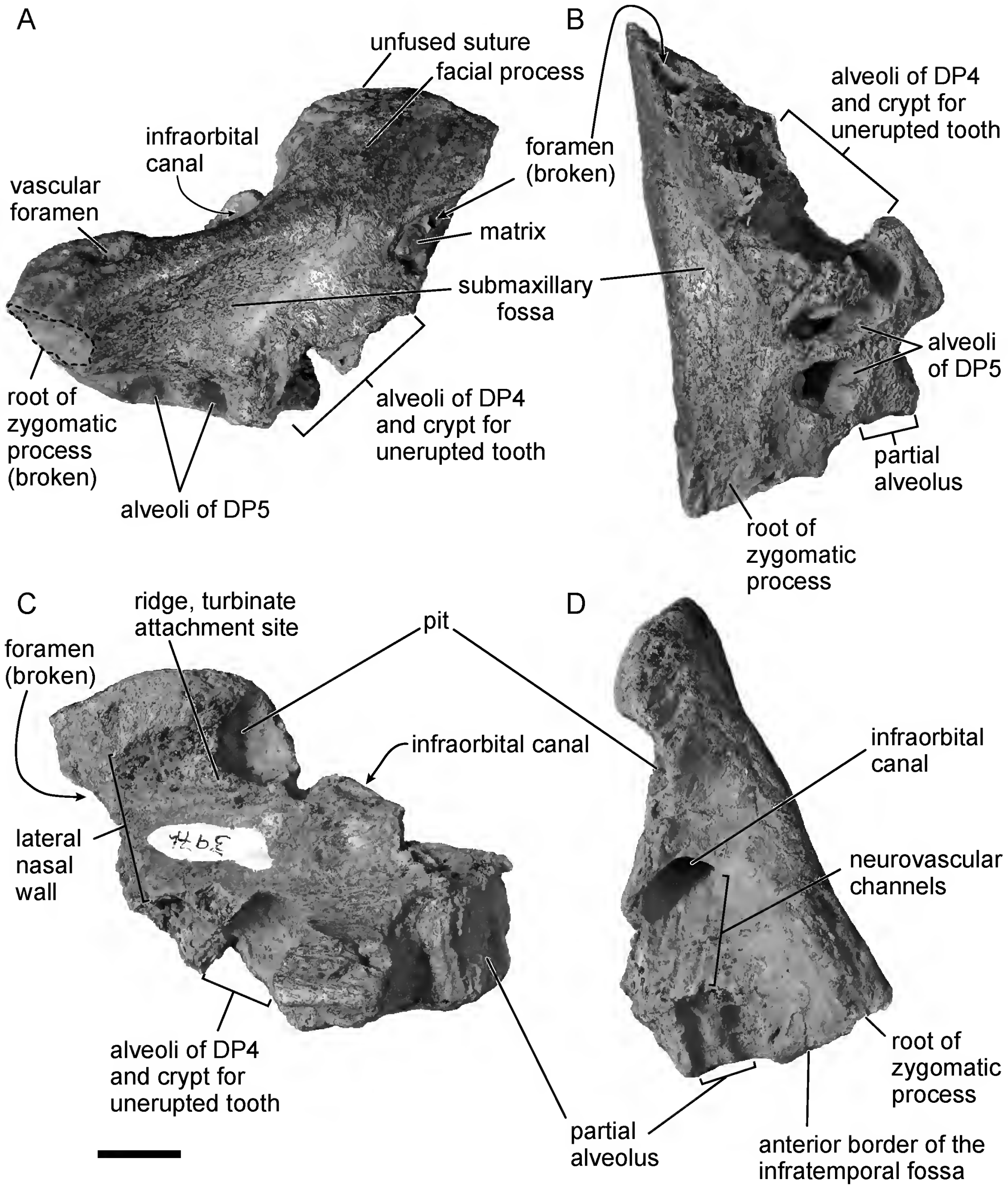


FIGURE 80. Right maxilla (CNRST-SUNY 397b) of a "plesielephantiform" proboscidean from the Eocene Tamaguélelt Formation, Mali in **A,** lateral; **B,** inferior; **C,** medial; and **D,** superior views. Dental nomenclature follows O'Leary et al. (2013). Scale bar = 1 cm.

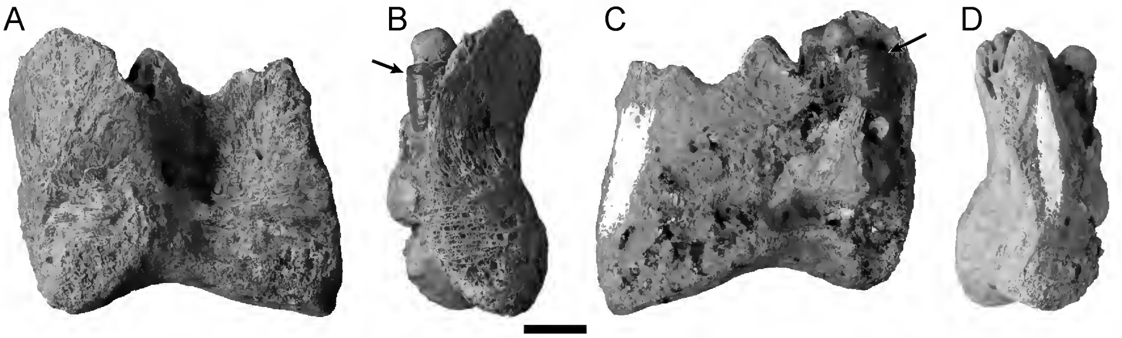


FIGURE 81. Fragmentary distal ?ulna, probably a left side, of a "plesielephantiform" proboscidean (CNRST-SUNY 606) from the Eocene of the Tamaguélelt Formation, Taoudenit Basin, Mali, in **A,** medial; **B,** cranial (arrow = embedded vertebrate coprolite from phosphatic matrix, also visible in C); **C,** lateral; and **D,** caudal views. Scale bar = 1 cm.

significant part of the matrix where this specimen was collected (Tapanila et al., 2008).

Discussion: We compared the new Malian maxillary specimen to several fossil proboscidean species collected from the Fayum localities in Egypt and casts of extinct Moroccan proboscideans. It is noteworthy that the texture of the bone in the Malian maxillary specimen is generally better preserved than specimens from these other localities and retains excellent surface detail. Two specimens help bracket the size range of the Malian maxilla. AMNH 13430, an adult *Moeritherium trigodon*, preserves regions similar to those in the Malian specimen, only the latter is much smaller. By contrast, comparisons with AMNH 127719, a cast of the maxilla of *Phosphatherium escuillei* (Gheerbrant et al., 1996) and also an adult individual, indicates that the Malian species was distinctly larger. Previously described proboscidean specimens from Mali (O'Leary et al., 2006) have consisted of dentaries, not maxillae, however, we note that the alveoli in those dentaries are comparable in size to the alveoli in this new maxillary specimen.

The Malian specimen compares closely in some important respects with AMNH 13458, *Phiomia wintoni*, a right maxilla of a subadult with a DP2, DP4, DP5, and an erupting M1. AMNH 13458 has a similar-sized posterior opening of the infraorbital foramen and is relatively robust compared to the Malian specimen. The two specimens differ in that the Malian specimen has a less flaring anterior root of the zygomatic process (when viewed superiorly), its alveolar process is shallower under the posterior opening of the infraorbital canal (when viewed laterally), and it has a more distinct submaxillary fossa. In comparing the two specimens in inferior view and aligning the posterior openings of the infraorbital canals, it appears that the large and broken crypt in the Malian specimen corresponds to the DP4 position of AMNH 13458, which would suggest the two more posterior alveoli would have corresponded to a missing DP5. AMNH 13458 also has an unfused bony suture that would have met the corresponding left maxilla in life. This suture corroborates the simultaneous coexistence of unfused cranial sutures with deciduous dentitions in these taxa, thus helping confirm that the Malian specimen, which has unfused cranial sutures but no teeth, represents a subadult.

The fragmentary ulna compares closely in both size and shape with a complete specimen from the Eocene of Libya described by Court (1995: fig. 5) and attributed to *Numidotherium savagei*. This fragmentary Malian ulna appears to have had a laterally compressed shaft, which Court (1995) mentioned as characteristic of *N. savagei*.

All the Malian specimens are extremely fragmentary and their significance lies primarily in expanding the geographic range and diversity of known early Paleogene African placental mammals. Along with the fossil hyracoid described above, the new proboscidean may be among the oldest paenungulates from Africa where they would have lived in an ancient tropical, nearshore environment (O'Leary et al., 2006). Both hyracoids and proboscideans are hypothesized to have been herbivorous (De Blieux and Simons, 2002; Clementz et al., 2008), and these early proboscideans may have been semiaquatic (Liu et al., 2008).

Several older reports exist of other fossil proboscideans from Mali. A report and illustration of isolated *Moeritherium* teeth from a well at In Tafident, 60 km northeast of Gao, from the Continental Terminal Formation (Arambourg et al., 1951) described what are likely the youngest known Malian mammal fossils from the early Paleogene (post-Ypresian). A later report identified, but did not illustrate, edentulous mammal remains from the locality Tamaguélelt and from the Tamaguélelt Formation (Lavocat, 1953).

PALEOECOLOGY AND CHANGE THROUGH TIME

Paleoecological Reconstruction

Descriptions above of the fossils found to date are the basis for our reconstructions of how certain key species from the Trans-Saharan Seaway looked in life (frontispiece). We have also set these species in a schematic ecosystem deriving details from both the sedimentology and the paleobiology (plate 2). In the Trans-Saharan Seaway, mangrove swamps lined shallow seas adjacent to the steep Adrar des Iforas massif from which numerous ancient rivers carried fresh water and sediment into the epeiric sea. The waters were warm and tropical, an inference supported particularly strongly by the mollusk fauna. Apex predators such as large fishes, sea snakes, and crocodyliforms existed in brackish water near shore, part of extensive coastlike ecosystems that lay deep within continental West Africa. The environment consisted of stable climate as indicated by temperature bioproxies such as fossilized wood. Our fieldwork has produced little evidence to support the idea that there was an ancient dry climate in this region of Mali as previously argued (Petters, 1977). We have not observed sedimentary indicators of aridity such as evaporites or aeolian sandstones (McKee, 1964; Hallam, 1985). Within a humid tropical setting, water lost through high evaporative conditions along the broad, shallow coast was likely replenished by shoreward flow of offshore waters. During times of high sea level, this strong evaporative pumping may have contributed to cycling of nutrient rich but oxygen poor offshore waters to deliver the unusual chemistry necessary for phosphogenesis that we have described (Tapanila et al., 2008).

Modern coasts are zones of interaction between terrestrial and aquatic realms, where, in the tropics, erosion from land intersects episodes of dramatic, hurricane-type weather originating at sea. We have identified lithological evidence of storm-generated turbulence in Trans-Saharan Seaway sediments—in the phosphatic conglomerate facies (Facies 5) and in shale/marl facies (Facies 3) (Tapanila et al., 2008)—even though both groups of sediments were far from the open ocean at the time they were deposited. Investigators have speculated about ancient ocean circulation patterns through modeling, but have not demonstrated a clear mechanism to generate cyclonic systems capable of forming major hurricanes inland (Kauffman, 1984; Nicholls and Russell, 1990; Lehman, 1997; Lehman, 2001). Evidence for severe and anomalous storm events has been identified in the sedimentary record (Roberts et al., 2008), however, for the Malian rocks we have yet to identify such event beds.

Modern tropical rainforests and reefs are particularly noteworthy for their biodiversity and species richness (Wilson, 1992; Bianconi, 2002). By analogy, the paleotropical Trans-Saharan Seaway was likely to have been among the more biodiverse parts of the Late Cretaceous–early Paleogene Earth based on the range of taxa we have described. Given the estimated shallow depth of the Trans-Saharan Seaway (50 m), we believe it effectively consisted of neritic and benthic zones only, such that all the waters would have been penetrated by sunlight. Evidence from the mollusk fauna, particularly taxa such as Ostreida, *Venericardia*, Turritellidae, Carditidae, Cerithioidea, Cypraeoidea, and Strombidae, point directly to the shallow sea being warm.

As emphasized by Harries (2009), the sedimentation of epeiric seas results from an interplay between siliciclastics from land and limestone creation in situ in marine waters, with the latter being the dominant method of rock formation. The five facies we have described show varying degrees of these two sedimentation types alternated and repeated through time as the sea transgressed and regressed (plate 1; figs. 13, 14). Near shore (proximal) sediments are dominated by sandstones, siliciclastic sediments that would have eroded from the adjacent Adrar des Iforas. The deepest water limestones that formed distal or basinward precipitated in situ, most likely from calcareous plankton (including nanoplankton and other algae, as well as benthic and planktic Foraminifera) and calcareous macroalgae. The tropical paleolatitude of Mali also encouraged carbonate production through algal mineralizations, with mudstones and shales developing under a mixture of these forces.

The ecosystem that we hypothesize was present in and along the Trans-Saharan Seaway included primary producers for which direct fossil evidence has been recovered, such as mangrovelike woody plants as well as species of Ostracoda (e.g., Damotte, 1991; Damotte, 1995; Colin et al., 1997), and Foraminifera (Krasheninnikov and Trofimov, 1969; Berggren, 1974; Bellion et al., 1989; Damotte, 1991; Berggren and Pearson, 2005). The primary consumers were filter-feeding invertebrates, including Ostreida, such as those that formed colonies on carcasses of dead turtles (described above), bivalve mollusks that burrowed into lithified coprolites and bone, and crabs, recognized by us from indirect evidence of fossilized burrows, as well as herbivorous hyracoid and plesielephantiform mammals (De Blieux and Simons, 2002; Clementz et al., 2008). Secondary consumers would again have included Ostracoda and Foraminifera among microscopic taxa, as well as larger species, such as pycnodont, amiid, osteoglossid, and siluriform fishes, and medium-sized snakes (e.g., *Amananulam*), all of which preyed on invertebrates or smaller vertebrates, and were themselves also consumed by tertiary consumers. Tertiary consumers, also called apex predators, included such species as dyrosaurid crocodyliforms, palaeophiid snakes, and sharks and rays, with direct evidence of their feeding present in the ichnofossils that we have collected (Hill et al., 2015). Remains of leaves, birds, and insects are conspicuously absent from the known fossils of the Malian Trans-Saharan Seaway that we have collected to date.

The apex predators are particularly well represented in the fossil record. We have reconstructed the palaeophiids as living in nearshore environments, where their fossils are typically found, often associated with mangroves and estuaries (Rage et al., 2003; Parmley and DeVore, 2005; Houssaye et al., 2013). They are known, for example, from similar nearshore fossil deposits of the Fayum (Andrews, 1901; 1906; McCartney and Seiffert, 2016), and are comparatively rare in sediments interpreted as pelagic or open ocean (Hutchison, 1985; Holman et al., 1990; McCartney et al., 2018). Our data are consistent with the hypotheses that the genus *Palaeophis*, known from Mali, was probably not pelagic (Hoch, 1975), and the nigerophiids would also have lived nearshore as they are elsewhere recovered in presumed freshwater or brackish deposits (Rage and Prasad, 1992; Rage et al., 2004; Rage and Dutheil, 2008; LaDuke et al., 2010; Pritchard et al., 2014).

Fishes recovered from the Malian field area underscore the challenge of determining whether an extinct taxon lived in fresh or saltwater, or both. The fossil fish taxa we have collected that were likely to have lived in freshwater in life include the Claroteidae or catfish (Siluriformes), and the Lepidosirenidae (Dipnoi) or lungfish. The fully marine taxa were the Chondrichthyes, the Pycnodontidae, and the Osteoglossidae. The Amiidae were potentially anadromous. The Malian lungfish belong to a clade that has a single living species, which is a generalized predator and omnivore restricted to freshwater (Myers, 1938). Marine records of Dipnoi are now limited to those that predate the Mesozoic (Heinicke et al., 2009; Otero, 2011). Thus, we conclude that the presence of a lepidosirenid in the Malian deposits is a bioproxy indicating the presence or proximity of freshwater sources entering the Trans-Saharan Seaway.

Myliobatiformes (stingrays) and other chondrichthyans (e.g., various sharks) recovered were all likely marine taxa based on comparisons with their living relatives. The extinct stingrays may have traveled in shoals or schools at high speeds, given the widespread nature of this behavior in their living relatives (Nursall, 1996a; Pavlov and Kasumyan, 2000). Torpediniformes (i.e., electric rays) were semipelagic to benthic fish that would have traveled in groups of smaller numbers (Claeson et al., 2014; Marramà et al., 2017), and sawfishes were also open marine to benthic taxa (Wueringer et al., 2009). Closely related extant stingrays, with crushing pavementlike dentition, are known to pursue hard-part prey, whereas torpediniform electric rays and sawfishes primarily consume softer prey (Summers, 2000; Wueringer et al., 2009; Claeson et al., 2014).

The Tethys Sea is considered to have been the center of origin for pycnodont fishes, as well as the site of their major radiation and last appearance (Poyato-Ariza, 2005), with the clade having undergone a multidirectional dispersal between the Tethys and the southern Atlantic (Nursall, 1996a). Pycnodonts were omnivorous benthic foragers and, as compared with halecostomes, are thought to have been capable of biting and/or nipping in combination with suction feeding to acquire a broad range of shelled invertebrates (Kriwet, 2001). The intriguing molariform teeth of these fishes indicate durophagous or ominivorous diets that would have included a range of benthic species such as "sponges, algae, zoanthids, coral, polychaetes, and other invertebrates" (Poyato-Ariza, 2005: 177). The Late Cretaceous and the modern African fish faunas, have both been described as homogenous for marine and freshwater fishes (Murray, 2000; Otero, 2010), a pattern that might be explained by the low topography across much of the African continent favoring movement of fish species among basins. The precise data on fish species by locality that we have supplied here contributes important new information for further continentwide assessments.

Finally, we note that scleractinian corals are absent from the Malian localities described here. While this may be a taphonomic idiosyncrasy, an environmental explanation for this finding is that Trans-Saharan Seaway waters were not adequately saline to support corals. The sea was highly likely to have varied in salinity under the opposing influences of the precipitation and drainage of freshwater, and the influx of open ocean saltwater. Scleractinian corals are typically stenohaline and cannot thrive outside normal marine salinity (Ferrier-Pagès et al., 1999; Hédouin et al., 2015), however, exceptions to this generalization have been reported (Chartrand et al., 2009). Another explanation for the observed lack of corals may be that the sea exhibited high turbidity, especially during the deposition of carbonates (marls), that would have blocked light to and clogged the feeding apparatus of these animals, thereby selecting against their existence. The micritic nature of the carbonates and abundance of interbedded shale facies amongst the carbonate beds lends support to this idea.

BODY SIZE IN CERTAIN EXTINCT PREDATORS

As epeiric seas experienced episodes of geographic isolation with changing sea level, the species they supported may have been under increased allopatric speciation pressures (Harries, 2009). Bodies of water cut off from the Tethys Sea had the potential to become centers of endemism. It is worth considering how such

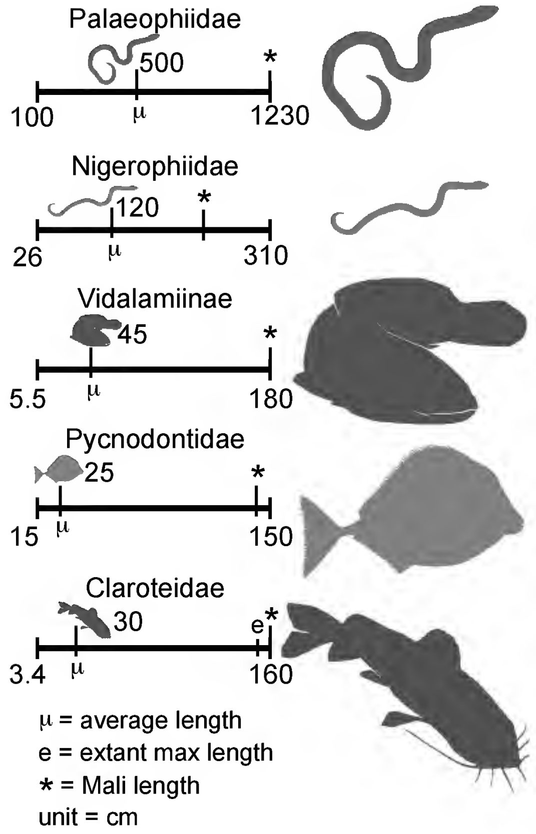


FIGURE 82. Certain extinct predators from the Trans-Saharan Seaway exhibited relatively large body length for their clades. In five cases the Malian representative is the largest or close to the largest member of the clade. Body-length ranges in a clade are indicated by black bars. Silhouettes compare the relative size of the average clade body length to the body length for the Malian fossil (clades not shown at actual size). The Malian fossils compare as follows: Paleophiidae: small: ~100 cm, average: ~500 cm, Mali: 1230 cm (~2.45 × average and largest in clade); Nigerophiidae: small: ~ 26 cm, average: ~120 cm, Mali: 210 cm (~1.75 × average), large: 310 cm; Vidalamiinae: small: 5.5 cm, average: 45 cm, Mali: 180 cm (~ 4 × average and largest in clade); Pycnodontidae: small: 15 cm, average: 25 cm, Mali: 122 cm (~ 4.8 × average), large: 150 cm; and Claroteidae: small: 3.4 cm, average: 30 cm, extant maximum length: 150 cm; Mali: 160 cm (~5.33 × average and largest in clade). For Pycnodontidae the comparison includes the length of the caudal fin in all species. Measurements and methods of deriving estimated lengths of extinct species provided in the Systematic Paleontology section.

environmental pressures may have impacted the important life history variable of body size in Trans-Saharan Seaway species. Full clade-by-clade consideration of this topic is beyond the scope of this paper, however, we note that body size appears to have been relatively large for several of the recovered fossil predators, including apex predators: sea snakes, amiids, pycnodonts, and siluriforms (fig. 82).

It has been observed that during the Eocene a major proliferation of large pelagic predatory fish occurred in the oceans (Friedman and Sallan, 2012), and our observations indicate this pattern may have extended to this epeiric sea. As the Trans-Saharan Seaway began to recede for a final time during the Eocene, patches of isolated water may have become increasingly common, and the large embayment described within Mali (fig. 15F) could have been cut off from the main Trans-Saharan Seaway during this time. Species found in the Eocene rocks left behind include *Maliamia gigas*, which is relatively large compared to other amiids (Grande and Bemis, 1998), and the new unnamed Malian Eocene catfish that is larger than (and morphologically distinct from) other reported African giant catfish, including contemporary fossil species from Egypt (El-Sayed et al., 2017) and later-occurring species from the Miocene of Chad (Pinton et al., 2011). The Malian lungfishes are also relatively large compared to close modern relatives (Martin, 1995), as are the pycnodonts based on body-size estimates from teeth supplied above.

Regarding snake body size, McCartney et al. (2018) recently used regression analysis of vertebral size to estimate the body sizes of palaeophiids from Mali. The three known species of snakes from Mali, *Palaeophis colossaeus* (Palaeophiidae), *Amananulam sanogoi* (Nigerophiidae), and an indeterminate species, were all estimated to exceed 2 m in total length. The largest of these, *P. colossaeus*, is among the three largest known species of snakes to have ever lived, and its body size is exceeded significantly only by the boid *Titanoboa cerrejonensis* from the Paleocene of Colombia (Head et al., 2009). Although an estimate of body size has not been performed for all known nigerophiids, using the regression in McCartney et al. (2018), the vertebral dimensions of *A. sanogoi* are matched only by "*Nessovophis*" *zhylga* from the Eocene of Kazakhstan (Averianov, 1997; McCartney et al., 2018). The indeterminate fossil snake we discovered is of intermediate size between *A. sanogoi* and *P. colossaeus*, with an estimated length exceeding 5 m. Given that we have likely underestimated size, this indeterminate snake was also a relatively large species (McCartney et al., 2018).

Although the pattern is complex and it is premature to draw major conclusions, an intriguing hypothesis to consider is that these species may have experienced a phenomenon of regional gigantism in "aquatic islands," or relatively isolated parts of the epeiric seas. The so-called island rule describes such a phenomenon in terrestrial island settings in which large species tend to become dwarfs and small species become gigantic (Van Valen, 1973; Lomolino, 2005). Lomolino (2005:1684) described the reasons for the phenomenon of the "island rule" to be "limited insular resources, the paucity of interspecific competition and predation . . . and the challenge of dispersing to, but not emigrating from, islands." He concluded with a plea to investigate other "island-like ecosystems" for possible discovery of trends in body-size evolution (Lomolino, 2005: 1696). The Trans-Saharan Seaway may have effectively resulted in "aquatic islands" that emerged during geologically short-term shrinkage and expansion of saltwater bodies. Understanding whether our report here constitutes a strongly supported pattern requires further investigation as to whether these species evolved in situ as a response to fragmented aquatic environments. Clade-by-clade phylogenetic comparisons with fossils sampled through their stratigraphic and geologic ranges will also be critical to the evaluation of this hypothesis. We note, for example, that palaeophiid snakes are large bodied across their known distribution, which may or may not have consisted of fragmented nearshore saltwater habitats.

Cretaceous-Paleogene (K-PG) Boundary

At the transition between the Maastrichtian Ménaka Formation and the Paleocene Teberemt Formation our section spans the K-Pg boundary. As described above, there appears to be a hiatus of nondeposition at this transition, which currently limits high-resolution stratigraphy across the boundary (plate 1). Smith and Jeffery (2000) suggested that carbonate platform drowning in the Paleocene might have disrupted sedimentation on a large scale, providing a possible mechanism to explain this hiatus. Alternatively, there is a global sea-level fall at or just below the K-Pg boundary (e.g., Haq, 2014) that could explain this unconformity and that is consistent with the original work of Radier (1959; see also Damotte, 1991; Moody and Sutcliffe, 1991, 1993) and the karstic nature of the uppermost Maastrichtian limestone bed in the region ("Terrecht I"). Lack of this important part of the section currently limits our ability to investigate such phenomena as eustasy-based extinctions, which has been proposed for the Mesozoic of the Western Interior of North America (Eaton et al., 1997).

Nonetheless, by placing extinct species in a phylogenetic and stratigraphic context we have been able to develop an improved picture of clade diversity through time in the Late Cretaceous–early Paleogene of West Africa, an area for which there has been a paucity of vertebrate fossils tied to detailed stratigraphic sections in this interval. We provide here some comments on two related questions: is the global pattern for a given clade one of species change or stability across this boundary, and, does the Malian fauna conform to or diverge from this pattern based on the evidence to date?

Limited inferences can be made about Malian placental mammals, which are very rare. We can report simply that, to date, they are found only on the Paleogene side of the K-Pg boundary and in Eocene rocks. It has been estimated that the placental mammal subclade Afrotheria had a substantial Cretaceous existence (e.g., Meredith et al., 2011), however, our direct paleontological work here, and broader combined data analyses, have not corroborated this estimate (O'Leary et al., 2013). The Malian fieldwork contributes some direct negative evidence, albeit localized, to the hypothesis that placental mammals are absent from Mesozoic rocks, even in Africa.

The K-Pg event had a catastrophic effect on the clade Archosauria, with the extinction of pterosaurs, nonavian dinosaurs, and many clades of crocodyliforms (MacLeod et al., 1997). By contrast, dyrosaurids have long been recognized as having representatives on both sides of the K-Pg boundary (Buffetaut, 1978a; Buffetaut, 1979). Minimally, the genus *Hyposaurus* occurs in Cretaceous and Paleogene strata (e.g., MacLeod et al., 1997). Jouve et al. (2005b) showed in a phylogenetic analysis of dyrosaurids that the majority of clade diversification occurred in the Maastrichtian or early Paleocene, even as other clades faced mass extinction globally. Our prior research further refined the timing of this diversification, and showed that as many as six dyrosaurid lineages arose in the Cretaceous and survived the K-Pg event (Hill et al., 2008). This result, based directly on fossils of a given taxon being found on either side of the boundary, provides further evidence for robust clade survivorship across this global mass extinction event. Moreover, even more dyrosaurid lineages are inferred to have crossed this boundary based on ghost lineages implied by the phylogenetic hypothesis (Hill et al., 2008: fig. 7).

This pattern prompts the question of why dyrosaurids appear to have survived the K-Pg event when other marine reptiles (e.g., mosasaurs and plesiosaurs) became extinct. (We note here that in one of our prior papers [Hill et al. 2008], we erroneously suggested that other marine crocodyliforms, e.g., metriorhynchids and teleosaurids, also became extinct at this time; these clades were already extinct before the Late Cretaceous [Markwick, 1998]). Several factors may be responsible for such differential survival including geographic range, eurytopy, and specialized feeding or reproductive strategies (Fara, 2000: and references therein). Jouve et al. (2008) proposed that dyrosaurid juveniles may have begun life in freshwater habitats, as do modern saltwater crocodiles, a life history strategy that would have been possible along the ancient Trans-Saharan Seaway. Such behavior may have afforded dyrosaurids a freshwater refuge unavailable to other marine reptiles. Another behavioral advantage for the clade may have related to the mode of locomotion employed by dyrosaurids. Data from CT scans of Malian dyrosaurid skulls (archived in MorphoBank Project 2735; www.morphobank.org) showed a vestibular morphology similar to that of turtles that preferentially locomote by walking along the floor of an aquatic habitat, rather than swimming in the water column (Georgi, 2006). If this behavior was present in dyrosaurids, it could be a factor in their survival relative to that of other swimming or fully terrestrial forms.

Our GPlates reconstructions of the shape and extent of the Trans-Saharan Seaway (fig. 15) are consistent with the global pattern of dyrosaurid dispersal proposed by Hastings et al. (2011). Those authors postulated an initial, northerly dispersal of dyrosaurids from Africa to the New World during or before the Late Cretaceous, with subsequent dispersal taking place along more southerly routes. Our Trans-Saharan Seaway reconstruction shows an open northerly route of dispersal for dyrosaurids in the Maastrichtian. By the Danian, the Trans-Saharan Seaway was also open to the south, a change that could have facilitated later dispersals of dyrosaurids to South America.

Unlike dyrosaurids, Malian turtle fossils that can be taxonomically assigned are currently found on the Paleogene side of the boundary only. They are members of Pleurodira (side-necked turtles), and within that clade, are part of the clades Pelomedusoides and its subclade Bothremydidae. A comprehensive review of the pelomedusoids organized the Malian specimens further into the tribe, Taphrosphyini, and showed that it contained two unnamed clades: one of *Nigeremys* and *Arenila*, and one of all other taphrosphyins, including two Malian specimens: the sister taxa *Azabbaremys* and *Acleistochelys* (Gaffney et al., 2006: figs. 1, 288; Gaffney et al., 2007). The species in the clade of *Nigeremys* + *Arenila* are found in Upper Cretaceous rocks, but members of the other clade in Taphrosphyini are found in Paleocene or younger rocks. One possible explanation for this pattern is that a single taphrosphyin lineage survived the K-Pg event and underwent significant diversification in the early Paleogene. This hypothesis could be tested by looking for more pelomedusoid specimens on both sides of the boundary in Mali and Niger, given the substantial facies continuity across the boundary.

The global effect of K-Pg extinction on snakes is poorly understood, with some evidence supporting a significant extinction event among terrestrial species (Longrich et al., 2012). The impact of this event on aquatic snake clades, however, is even less well understood. Only three palaeophiid taxa have been reported prior to the K-Pg boundary—all from Africa (Rage and Wouters, 1979; Lingham-Soliar, 1998; Rage and Werner, 1999). Of these, the date of one has been called into question (Head et al., 2005), and another has not been properly described or figured (Lingham-Soliar, 1998). However, if any of these occurrences is accurate, it would suggest that the clade Palaeophiidae survived the K-Pg event and diversified in the Paleogene. More than 20 species are known from the Paleocene and Eocene globally and the Eocene palaeophiid specimens that we have recovered further document the post-K-Pg diversity of this clade (McCartney et al., 2018). Nigerophiids, however, occur as early as the Cenomanian (Rage and Dutheil, 2008), and approximately equal numbers of these rare fossil species have been found on either side of the K-Pg. The Cretaceous records include a number of presumed freshwater species (Rage and Prasad, 1992; Rage and Werner, 1999; Rage and Dutheil, 2008; LaDuke et al., 2010; Pritchard et al., 2014), and later, marine species occur in the Paleocene (Rage, 1975) and Eocene (Rage, 1980; Averianov, 1997; McCartney et al., 2018). Our findings provide an additional Paleocene datapoint for nigerophiids but no further information about the K-Pg survivorship of this clade. Because there is both fresh- and saltwater influence at the locality that produced nigerophiids it is not clear at present whether our Paleogene species preferred a particular environment.

Globally, the K-Pg event did not result in a mass extinction of fishes (Cavin, 2001). Instead, the event appears to have punctuated certain larger trends of slow, background extinction already underway by the Late Cretaceous (Friedman and Sallan, 2012; Sibert and Norris, 2015; Poyato-Ariza and Martín-Abad, 2016). Our findings in Mali show an overall pattern of replacement of cartilaginous fishes by bony fishes at this boundary, which we now discuss in more detail.

Generally, Cretaceous rocks preserve more nonbatoid chondrichthyans (e.g., sharks) than osteichthyans, whereas the reverse is generally true for the Paleogene (Cavin, 2001; Friedman and Sallan, 2012; Sibert and Norris, 2015; Poyato-Ariza and Martín-Abad, 2016). For osteichthyans, Poyato-Ariza and Martín-Abad (2016) described a gradual, macroevolutionary pattern of competitive replacement of nonteleostean osteichthyans (e.g., pycnodonts, semionotiforms, stem-group teleosteans) by teleosts from the Mesozoic into the early Cenozoic and argued that the K-Pg event was of no particular consequence to this replacement. Moreover, significant changes to the chondrichthyan fauna also characterized the K-Pg boundary as species of nonbatoid chondrichthyans such as sharks were abundant in the Cretaceous but dropped in numbers relative to osteichtyhans recorded in similar environments in the Cenozoic (Friedman and Sallan, 2012; Sibert and Norris, 2015).

Several authors have reported that the majority of osteichthyan and chondrichthyan fishes that went extinct during the Maastrichtian, or at its end, were marine fishes, while the majority of freshwater- and brackish-environment fish survived the K-Pg boundary (Cavin, 2001; Friedman and Sallan, 2012; Sibert and Norris, 2015). Those authors also indicated that the species most negatively affected by this event were fast-swimming and piscivorous predators (Cavin, 2001; Friedman and Sallan, 2012; Sibert and Norris, 2015).

The aforementioned pattern of replacement (teleosts supplanting large, pelagic, marine fishes, many of which were chondrichthyans) is not entirely reflected in the data from Mali. For example, Cretaceous Malian lungfish and pycnodonts represent clades that survived the K-Pg boundary and are also recovered from the Paleogene rocks of Mali. Additionally, osteichthyans such as claroteid catfishes and vidalamiine bowfins persist into the Eocene of Mali. Globally the fossil record shows that pycnodonts and amiids were declining by the Late Cretaceous, with the diminishing diversity of the clades not particularly impacted by the K-Pg boundary (Poyato-Ariza and Martín-Abad, 2013). In Mali, *Pycnodus jonesae* and *Pycnodus* sp. are found in rocks on both sides of the K-Pg boundary and we do not observe a marked diminishment of species post K-Pg. The addition of vidalamiine bowfin and claroteid catfishes to the Paleogene Malian fauna underscores an overall pattern of increasing diversity of osteichthyans without a pronounced faunal turnover. Of note is that these osteichthyans all have a known (from extant relatives), or hypothesized, brackish and/or freshwater life history, a strategy that has been linked with high survivorship across the K-Pg boundary (Cavin 2001; Friedman and Sallan, 2012).

Sibert and Norris (2015) showed a global pattern of faunal turnover around the K-Pg boundary as osteichthyan species filled ecological niches recently vacated by cartilaginous fishes. Given the observed rise in the number of osteichthyan species in Mali, we should expect a corresponding decrease in cartilaginous fish. Our observations, albeit preliminary, support this prediction. In the Cretaceous of Mali, the chondrichthyan fauna is relatively diverse, consisting of two genera of sclerorhynchid sawfish, the myliobatid stingray *Myliobatis*, and the lamniform shark *Serratolamna*. In contrast, only *Myliobatis* survives the K-Pg globally but is not actually represented in any of the Paleogene records of Mali (Claeson et al., 2010). In the Paleogene of Mali, the Eocene torpediniform electric ray *Eotorpedo* is the only cartilaginous fish that is recovered. Thus, among fishes at the K-Pg transition in Mali, the trend is one of replacement and overall net decrease in chondrichthyans relative to osteichthyans. It is noteworthy that the Cretaceous and Paleogene chondrichthyans were all considered pelagic, fast-swimming, piscivorous predators that may have spent part of their time near the shore.

Of the invertebrate fauna, there are only two mollusk-producing beds in the Upper Cretaceous part of our section, each with a handful of poorly preserved taxa, mostly identified only to the family level or higher. Thus, although we have quite a few Paleogene mollusk specimens and localities, it is premature to draw conclusions about effects of the K-Pg event on molluscan diversity in the Malian Trans-Saharan Seaway, beyond the observation of a general pattern of persistence of higher clades. In the Paleogene Malian fauna, the Ostreida, *Venericardia*, and Turritellinae mollusks remain common, and we hypothesize that broadly similar environmental and taphonomic conditions persisted in the Trans-Saharan Seaway through the Cretaceous into the Paleogene.

Of the echinoid species we have collected, none occurs on both sides of the K-Pg boundary in our sections. The regular echinoid, *Echinotiara* occurs in Upper Cretaceous beds, and the irregular echinoids *Linthia* and *Oriolampas* occur in Paleocene beds. Jeffery (2001) reported that the spatangoid heart urchins, in general, were less severely affected by the K-Pg extinction than some other echinoid clades. For example, *Linthia* is recorded from the Maastrichtian of Algeria and Oman (Cotteau et al., 1881; Smith, 1995) before dispersing more broadly in Africa, the Middle East, Europe, and North America in the Paleogene (Smith and Jeffery, 2000). Finally, palynological studies across the K-Pg boundary

(Boudouresque et al., 1982) documented an ongoing warm and humid climate, as well as the presence of mangrove forests.

Paleocene-Eocene Boundary and PETM

The Paleocene-Eocene boundary falls between the Teberemt and the Tamaguélelt formations in our section but stratigraphic resolution is currently very coarse. The warm global temperature spike known as the PETM would likely have fallen close to this formational transition but cannot at present be placed with precision. While our PETM interpretations are preliminary and in need of testing by additional collecting and higher resolution stratigraphy, a picture of significant faunal turnover does not emerge conspicuously from the data we have assembled so far. The Paleocene-Eocene boundary has been far less studied for the neritic realm than for the deep sea realm (Speijer et al., 1996), making new contributions on the neritic realm, such as we provide here, a critical new global datapoint for the paleotropics, if only to seed further work. By the Paleocene, and especially by the early-middle Eocene, the depositional environment of the Trans-Saharan Seaway developed an increasingly shallow-water signal. We hypothesize that the remaining saltwater embayment had probably become cut off from the open ocean as the Trans-Saharan Seaway retreated northward. The water in the relict intracratonic sea then likely verged on having a brackish to increasingly freshwater composition.

No Paleocene mammal fossils have been found in Mali, and only a small number of fragmentary paenungulates have been found in the Eocene sediments as noted above. Likewise, the best-preserved turtle specimens from Mali are Paleocene. Those turtles at our single, vertebrate-producing Eocene locality, Tamaguélelt (locality Mali-20), are so fragmentary as to be of uncertain attribution, and thus, little can be said presently about turtle or mammal diversity across the PETM.

Regarding dyrosaurid crocodyliforms, Hill et al. (2008: fig. 7) showed that approximately half as many dyrosaurid lineages survived the Paleocene-Eocene boundary as survived the K-Pg boundary (note, however, that this figure erroneously showed the two species of *Rhabdognathus* extending into the Eocene; the youngest occurrence of this genus is Paleocene [e.g., Jouve, 2007; Hastings et al., 2011]). By the end of the Eocene, all dyrosaurids had gone extinct, the youngest record being a few fragments from the Upper Eocene of Myanmar (Buffetaut, 1978b). Moody and Sutcliffe (1990: 22) recognized similarities between Eocene (Ypresian) crocodyliform species from the Iullemmeden Basin of Mali and those from South America, raising the possibility that dyrosaurids were still in wide marine circulation globally at least through the early Eocene. This hypothesis is problematic, however, because diagnostic dyrosaurid remains have yet to be found from Eocene rocks of the Americas. A phylogenetic analysis of Dyrosauridae by Hastings et al. (2011) revealed an African origin for the clade, with New World species nested among African taxa. These complex relationships are consistent with as many as three separate westward dispersal events beginning in the Late Cretaceous and ending by the early- to mid-Paleocene (Hastings et al., 2011). Still, transatlantic dispersal during the Eocene has been hypothesized for other vertebrate taxa (Houle, 1999; Vidal et al., 2007) and may also have continued for dyrosaurids.

Palaeophiid snakes demonstrated their highest global diversity in the Eocene with records from localities across the region of the ancient Tethys Sea (summarized by Rage et al., 2003), including Mali (Rage, 1983). However, of the approximately 20 named palaeophiid species, only one, *Palaeophis zhylan*, may have a Paleocene occurrence (Nessov and Udovitschenko, 1984). Palaeophiids then appear to have become extinct by the beginning of the Oligocene. As such, the clade appears to demonstrate a diversification following the PETM, at which time it became an important example of an apex predator in nearshore faunas. Nigerophiid snakes are far less common than palaeophiids at all times, and in the Eocene are known from only two marine species (Rage, 1980; Averianov, 1997). The general paucity of records of nigerophiids makes it difficult to discern larger patterns with respect to climatic changes and major faunal boundaries; however, we can say that the greatest nigerophiid diversity occurred prior to the PETM (and in fact prior to the K-Pg boundary). Specifically, in Mali, only three snake taxa are recorded: from the Paleocene, a member of Nigerophiidae (*Amananulam sanogoi*), and from the Eocene a member of Palaeophiidae (*Palaeophis colossaeus*) and a taxon of uncertain attribution (McCartney et al., 2018). Elsewhere in the Trans-Saharan Seaway, there are two other snakes reported: the nigerophiid *Nigerophis mirus* from the Paleocene of Niger (Rage, 1975), and the palaeophiid *Palaeophis africanus* from the middle Eocene of Niger (Andrews, 1924). Taken together, this pattern suggests that smaller nigerophiids occurred in the Paleocene and larger palaeophiids in the Eocene of the Trans-Saharan Seaway, but much further sampling is necessary to truly demonstrate this hypothesis.

In general terms, the fish fauna in Mali was becoming increasingly freshwater through the Eocene, an observation that coincides with the ultimate retreat of the sea from the region. Malian Eocene fish species (pycnodonts, amiids, catfish) tended to have relatively large body size for their respective clades, as noted above. Among the osteichthyans, our section documents that two pycnodontid species, *Pycnodus jonesae* and *Pycnodus* sp. survived the PETM because they are found in rocks on both sides of it. The other pycnodontid species, *P. zeaformis* and *P. maliensis*, occur exclusively in our Eocene localities. Pycnodontidae as a clade persisted only as late as the Eocene (Nursall, 1996b; Poyato-Ariza, 2005). Thus, the Malian specimens are among the latest-surviving species. Even though some lineages clearly survived the PETM, the clade as a whole did not thrive subsequent to it. Poyato-Ariza (2005: 182) specifically considered the Eocene pycnodonts in Mali to represent a "relict" population of the Atlantic. The Tamaguélelt Formation pycnodonts are most closely related to contemporary taxa from Monte Bolca, Italy (Poyato-Ariza and Martín-Abad, 2013).

Several other osteichthyans in the Malian fauna are found only in Eocene rocks. For example, the amiid *Maliamia* has only been found in Eocene rocks of the Tamaguélelt Formation, where it represents the last surviving species of Vidalamiinae. As this clade appears to have already been on its way to extinction by the early Eocene, our work provides no new information regarding how it was impacted by the PETM. Similar temporal restriction in the Malian fauna also describes the osteoglossid *Brychaetus*, already an outlier in its clade for being a marine osteoglossid. However, among the Dipnoi, we have directly documented the species *Lavocatodus giganteus* from Paleocene and Eocene rocks and no striking differentials of taxon or specimen counts accompany the PETM. *Protopterus elongus*, however, is known only from Malian Eocene rocks, thus providing no information about this faunal transition. The last appearance of *Lavocatodus* occurred in the Middle Eocene Tamaguélelt Formation. Finally, the Paleogene fauna is limited to the batoid *Eotorpedo*, an electric ray that was semipelagic. Thus, no general conclusions can be reached about the response of batoids to the PETM, and sharks were absent in the Paleogene, as discussed above. Malian catfish are known only from Eocene rocks, thus we cannot interpret how the PETM impacted this clade. Overall for fishes, there is a suggested pattern of large body size and freshwater tendencies emerging as the Trans-Saharan Seaway diminished.

Among the invertebrates, we do not recover echinoids that are younger than Paleocene in age. Indeed, Smith and Jeffery (1998) emphasized that after the Danian, low latitude, shallow-water carbonate deposits diminished greatly. Such an environmental shift would have restricted the paleoenvironment that supported many echinoid species. As Malian rocks preserve Paleocene angiosperm macrofossils, further collection up the stratigraphic section has the potential to yield important new data about tropical plant response to the PETM. Jaramillo et al. (2010) reported, based on a study of neotropical fossil pollen, that through this global warming event, plant diversity actually increased even with high temperatures and relatively high levels of atmospheric carbon dioxide. Further testing in other global regions of the tropics such as Mali will be important for evaluating this intriguing hypothesis.

Our examination of the mollusk diversity in the Malian Trans-Saharan Seaway shows no obvious differences between Paleocene and Eocene faunas, a pattern similar to that displayed in other subtropical regions in general (Sessa et al., 2012). Thus, at present, there are no obvious faunal effects of the PETM, there is simply evidence for the persistence of taxa with a preference for warm waters. There are several different Turritelline genera that are moderately abundant within the Paleogene Mali fauna, indicating a warm, shallow water signature (Allmon, 2007; 2011). Other Paleogene taxa within the Mali outcrops also display affinities for warm waters. These include several representatives of the gastropod families Volutidae and Cerithiidae, which today are most common within the tropics. Similarly, the Ostreida are found in modern tropical and temperate seas, and Pholadidae and Spondylidae are most common in these settings as well (Mikkelsen and Bieler, 2008).

Even though there is no striking pattern of change in mollusks through the PETM, we have new observations that indicate some differences between the Malian faunas and those of higher latitudes during the Paleogene. The gastropod families Strombidae and Volutidae, and the superfamily Cypraeoidea, and the bivalve families Pholadidae and Ostreidae are common and diverse components of the Paleogene Mali assemblage, and today these groups have a tropical to subtropical distribution. These groups were relatively less diverse in coeval subtropical regions of the early Paleogene. For example, comparisons with the well-studied faunas of the U.S. Gulf Coastal Plain (Sessa et al., 2012), show that a global greenhouse climate still resulted in biotas within tropical latitudes (like Mali) that were distinct from those in extratropical regions (like the U.S. Gulf Coast Plain), even though the latter experienced tropical temperatures (Sluijs et al., 2007). The Malian fauna instead shows stronger taxonomic affinities with nearby faunas in Nigeria, Egypt, and Saudi Arabia, which together form a truly tropical fauna.

CONCLUSIONS

Central questions in paleobiology often require rigorous and persistent fieldwork to amass high-resolution sedimentological, stratigraphic, paleontological, and taphonomic data for different regions of the world. Careful collecting of such "raw occurrence data" (Novacek, 1999: 231) can be tedious, taking years or even decades of fieldwork, involving a range of experts who simultaneously pursue detailed laboratory analysis in phylogenetic systematics, biostratigraphy, and computer-aided reconstructions of past environments. Of particular interest are raw occurrence data from stratigraphic sections that pass through major faunal boundaries or extinction events in deep time, which may be associated with adaptive radiations. For the K-Pg boundary and the PETM, two such faunal events, these kinds of sections with associated vertebrate fossils have not been easily identified in Africa (Archibald, 1996; Wing et al., 2005; Stevens et al., 2008; Schulte et al., 2010). We have attempted to build the foundation of such a section through our two decades of team-based work in Late Cretaceous–early Paleogene nearshore marine rocks of Mali, which we have synthesized here.

This monograph brings together our collection of and research on new invertebrate, vertebrate, ichno- and plant fossils, our measurement, correlation, and fundamental descriptions of new stratigraphic sections, and our studies of taphonomy and sedimentology and our subsequent laboratory analyses in phylogenetics, comparative anatomy, biostratigraphy, and sequence stratigraphy. This collection of rock and fossil material recording the existence of the ancient sea has yielded over 10 prior scientific research publications, which include the identification of new species and the description of sedimentary environments. At the time of this writing the field area is not accessible to scientists. The collection made from these expeditions nonetheless provides an enriched resource for ongoing paleobiological research.

The approximately 50 my existence of the Trans-Saharan Seaway fell within a time interval that has been identified as marking the rise of present-day ecosystems dominated by angiosperms and the rise of their complex interaction with vertebrate and invertebrate taxa (Novacek, 1999). With the work here we have described the extinct plants and animals of a West African paleoecosystem such that they can now be better compared to regions such as the important localities of the Western Interior of North America, which have been more intensively studied (Archibald, 1996). While our section currently includes a sedimentary hiatus close to the K-Pg boundary itself, much of the region still requires primary mapping and paleontological research that could produce more refined, and even complete, stratigraphy.

Future Work

Our fieldwork circumscribes several areas of future research that should be a priority once northern Mali is again accessible to scientists. Several Malian fossil-bearing localities are extremely rich and extensive but underworked. Paleocene localities that yielded complete fossil turtles form very extensive outcrops and have potential to yield other key vertebrate species. There is also high probability of future discoveries of fossil mammals from the phosphate conglomerates of Tamaguélelt with further surface collecting alone. This may produce discoveries impacting our understanding of the early diversification of placental mammals and an important paleontological test of model-based diversification estimates. Skull material of Paleogene fossil sea snakes remains elusive worldwide, but, given the large numbers of vertebral specimens in the Tamaguélelt Formation, the rocks there may also ultimately yield cranial material. It is also noteworthy that significant fossil discoveries in the region have been made in older stratigraphic units other than those that are the focus of this monograph. Exposures of the Continental Intercalaire crop out quite extensively in the Iullemmeden Basin. The western side of the Adrar des Iforas has produced a variety of fossils, including abundant petrified logs (*Metapodocarpoxylon libanoticum*) and a relatively limited continental vertebrate fauna of titanosaurian sauropods, turtles, fish, and crocodyliforms. These Early Cretaceous localities are each dominated by coarse-grained sandstones with less abundant pedogenically modified mudstones that we interpret to be fluvial channel and floodplain deposits. They await further paleobiological exploration.

This project was initiated and funded primarily as a fossil-finding expedition, and there remains a tremendous amount of descriptive and analytical work in sedimentary geology to be done in this area including refined biostratigraphy and exploration. The area presents an important opportunity for future chronostratigraphers to deploy new and creative methods to date this succession of rocks. Such work, however, requires greater security on the ground than existed during the expeditions described here to permit a more protracted period of scientific data collection. Further reconstruction of the ancient freshwater drainage patterns of West Africa using Malian rocks, would also expand our understanding of sedimentary formations, and species habitats and ranges, particularly of ancient fish. Such work could inform our understanding the ancient height of several Precambrian massifs such as the Adrar des Iforas. We have discussed above regional similarities between rocks in Mali and those in other areas covered by the Trans-Saharan Seaway such as Niger and Nigeria that warrant further exploration. There are also intriguing sedimentological and paleobiological similarities between the Malian Trans-Saharan Seaway rocks and more distant deposits such as those of the Umm Himar Formation of Saudi Arabia (Madden et al., 1995) that warrant further comparison.

Given the recurrent deposition of five different facies we have described in the Late Cretaceous–early Paleogene rocks of Mali, establishing the relative ages of these facies through time has always been extremely challenging. Thus, a major outstanding project is the study of onshore-offshore stratigraphy and facies change throughout the Iullemmeden and Taoudenit basins and the Gao Trench such that detailed hypotheses of the timing of transgressions and regressions can be increasingly refined. Coupled with efforts to sample the fauna more densely and precisely, such an undertaking would facilitate a test of such hypotheses as, for example, whether marine regressions tend to cause extinction among terrestrial vertebrates, or whether marine transgressions tend to impact freshwater species most negatively (Archibald, 1996). Finally, the rocks of Niger and Nigeria have been in many ways more extensively studied than those of Mali. Improved correlation among formations regionally and across international boundaries will be fundamental to developing a fully integrated picture of ancient life in the Trans-Saharan Seaway.

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APPENDIX 1

Expedition Teams by Year

Members of joint Centre National de la Recherche Scientifique et Technologique du Bamako, Mali and Stony Brook University, Stony Brook, New York, expeditions. Institutions for expedition members are those at the time of the expedition.

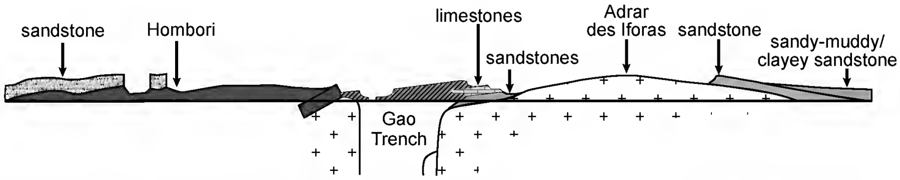
1999 team, top row left to right, Cal Lassana Soumaré (lead, Malian army), Eric Roberts (University of Montana), Mamadou Sanogo (driver and mechanic), Amadou Touré (Malian army), Mohamed Ag Fagaii (guide, Malian army), Seydou Doumbia (lead, driver and mechanic), Mamadou Bouaré (geologist, École Nationale des Ingénieurs, Mali), bottom row, left to right, Maureen O'Leary (expedition leader, paleontologist, Stony Brook University), Famory Sissoko (anthropologist, Institut des Sciences Humaines, Mali), Jason Head (paleontologist, Southern Methodist University), and Sidy Baba Adiawakoye (Malian Army).

2003 expedition team, top row from left, Famory Sissoko (anthropologist, Institut des Sciences Humaines, Mali), Mamadou Bouaré (geologist, École Nationale des Ingénieurs, Mali), Illy (Malian army), Youssuf (Malian army), Bou Traoré (driver and mechanic), Michael Novacek (paleontologist, American Museum of Natural History), Mohamed (lead, Malian army); bottom row from left, Eric Roberts (lead geologist, University of Utah), Leif Tapanila (geologist, University of Utah), Maureen O'Leary (expedition leader, paleontologist, Stony Brook University), Seydou (driver and mechanic), Mamadou Sanogo (driver, mechanic and logistics), Souleman (Malian army).

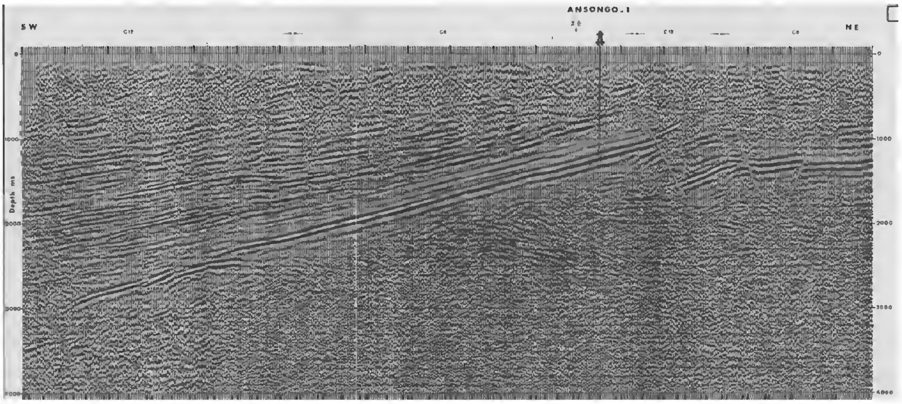
2009 expedition team, top row from left, Michael Novacek (paleontologist, American Museum of Natural History), Foudé Keita (driver and mechanic), Nafogo Coulibaly (anthropologist, Institut des Sciences Humaines), Jacob McCartney (paleontologist, Stony Brook University), Maureen O'Leary (expedition leader, paleontologist, Stony Brook University), Mamadou Sanogo (lead driver and mechanic), Leif Tapanila (geologist, Idaho State University); bottom row, left to right, Modibo Keita (driver and mechanic), Aldiouma Cissé (geologist, Faculté des Sciences et Techniques), Eric Roberts (lead geologist, James Cook University), Moussa Yatara (driver and mechanic).

APPENDIX 2

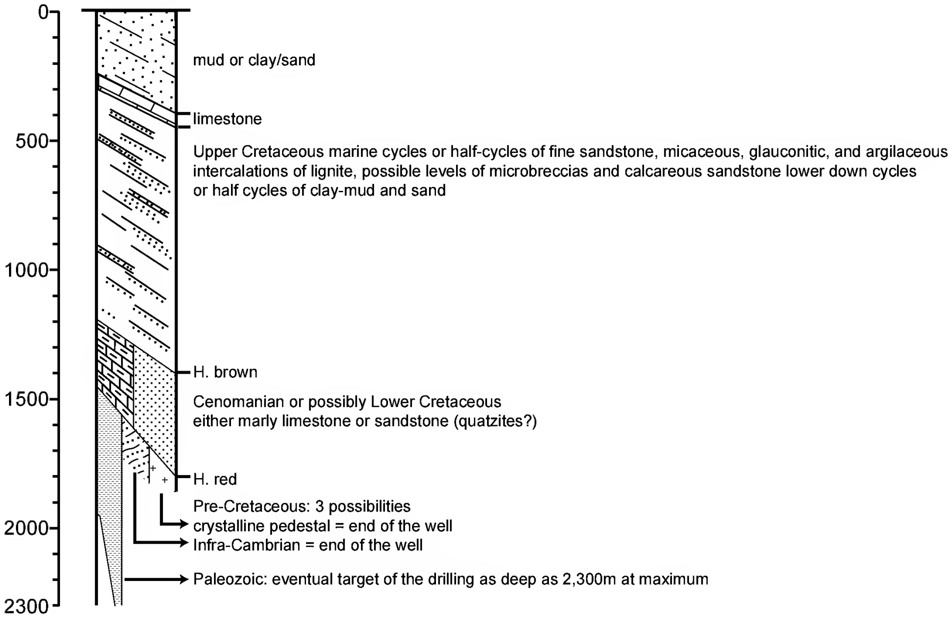
Well-log "Ansongo 1" (Elf-Aquitaine, 1979) that Bisected Sediments of the Gao Trench, Mali, with Schematic Map for Geographic Orientation.



A. Generalized cross-section after Radier (1959) showing the tectonic elements in Mali. Radier's diagram extends from southwest (left) to northeast (right) capturing the graben (or possibly half graben in places) that is the Gao Trench. The Adrar des Iforas are Precambrian rocks.



B. Interpretted Seismic Line-5 in the Gao Trench collected by Elf-Aquataine in 1979. Seismic line is roughly perpendicular to the basin axis along the line of the Ansongo-1 well (fig. 2). Faults in red are our interpretations.



C. Generalized well stratigraphy of the "Ansongo-1" well drilled by Elf-Aquataine, 1979.

APPENDIX 3

Sediment Samples Examined for Microfossils

All samples listed were analyzed for calcareous nannoplankton, and four were analyzed for palynomorphs.

Locality	**Palynomorphs**	**Calcareous nanoplankton**
Mali-1	not analyzed	none found
Mali-2	not analyzed	none found
Mali-7 unit 11	not analyzed	none found
Mali-7 unit 12	not analyzed	none found
Mali-8 sed sample	not analyzed	none found
Mali-11 sed sample	dinocysts absent; palynodebris present	none found
Mali-12 sed sample	not analyzed	none found
Mali-13 sed sample	not analyzed	none found
Mali-14 CT sand	not analyzed	none found
Mali-16 cobbles	not analyzed	none found
Mali-17 unit 2	not analyzed	none found
Mali-17 unit 3 hash	one dinocyst (*Spiniferites*) present, not identifiable to species	none found
Mali-18 unit 8 sed sample	not analyzed	none found
Mali-19 lower phosphates	dinocysts absent	none found
Mali-20 paper shale	not analyzed	none found
Mali-20, unit 3 sed sample	dinocysts absent	none found
Mali-21	not analyzed	none found

APPENDIX 4

AMNH Specimen Numbers

AMNH numbers assigned to Malian specimens mentioned in the text. As of 2019, the CNRST-SUNY collection of Malian fossils and sediment samples has been moved to the Department of Paleontology at the American Museum of Natural History, New York. Some specimens are more than one taxon (i.e., fish coprolite with mollusk boring).

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 2	22231	*Myliobatis wurnoensis*
CNRST-SUNY 3	22232	*Myliobatis wurnoensis*
CNRST-SUNY 4	22233	*Myliobatis wurnoensis*
CNRST-SUNY 5	22234	*Myliobatis wurnoensis*
CNRST-SUNY 6	22235	*Myliobatis wurnoensis*
CNRST-SUNY 7	22236	*Myliobatis wurnoensis*
CNRST-SUNY 8	22237	*Myliobatis wurnoensis*
CNRST-SUNY 9	22238	*Myliobatis wurnoensis*
CNRST-SUNY 10	22239	*Myliobatis wurnoensis*
CNRST-SUNY 11	22240	*Myliobatis wurnoensis*
CNRST-SUNY 12	22241	*Myliobatis wurnoensis*
CNRST-SUNY 13	22242	*Myliobatis wurnoensis*
CNRST-SUNY 14	22243	*Myliobatis wurnoensis*
CNRST-SUNY 15	22244	*Myliobatis wurnoensis*
CNRST-SUNY 16	22245	*Myliobatis wurnoensis*
CNRST-SUNY 17	22246	*Myliobatis wurnoensis*
CNRST-SUNY 18	22247	*Myliobatis wurnoensis*
CNRST-SUNY 19	134683	*Libycoceras crossense*
CNRST-SUNY 37	22248	*Myliobatis wurnoensis*
CNRST-SUNY 38	22249	*Myliobatis wurnoensis*
CNRST-SUNY 39	22250	*Myliobatis wurnoensis*
CNRST-SUNY 42	22251	*Brychaetus*
CNRST-SUNY 43	22208	*Stephanodus lybicus*
CNRST-SUNY 45	22209	*Stephanodus lybicus*
CNRST-SUNY 46	22210	*Cretalamna maroccana*
CNRST-SUNY 47	22211	*Cretalamna maroccana*
CNRST-SUNY 48	22212	*Cretalamna maroccana*
CNRST-SUNY 49	22213	*Cretalamna maroccana*
CNRST-SUNY 50	22214	*Cretalamna maroccana*
CNRST-SUNY 51	22215	*Cretalamna maroccana*
CNRST-SUNY 52	22216	*Cretalamna maroccana*
CNRST-SUNY 53b	22220	*Onchopristis numidus*
CNRST-SUNY 53c	22221	*Onchopristis numidus*
CNRST-SUNY 53d	22222	*Onchopristis numidus*
CNRST-SUNY 53a	22230	*Schizorhiza stromeri*
CNRST-SUNY 54	22217	*Pycnodus jonesae*
CNRST-SUNY 56	22223	*Stephanodus lybicus*
CNRST-SUNY 57	22224	*Stephanodus lybicus*
CNRST-SUNY 58	22035	*Pycnodus* sp.
CNRST-SUNY 60a	22041	?Sparidae
CNRST-SUNY 60b	22042	*Eotrigonodon jonesi*
CNRST-SUNY 62	22036	*Onchopristis numidus*
CNRST-SUNY 63a	134575	*"Haustator"* sp.
CNRST-SUNY 63b	134576	*"Haustator"* sp.
CNRST-SUNY 63c	134577	*"Haustator"* sp.
CNRST-SUNY 63d	134578	?*Mesalia* sp.
CNRST-SUNY 69	22037	*Stephanodus lybicus*
CNRST-SUNY 70	22038	*Stephanodus lybicus*
CNRST-SUNY 72	134667	*Linthia sudanensis*
CNRST-SUNY 73	134668	*Linthia sudanensis*
CNRST-SUNY 74	134669	*Oriolampas michelini*
CNRST-SUNY 75	134670	*Linthia sudanensis*
CNRST-SUNY 76	134671	*Linthia sudanensis*
CNRST-SUNY 78	134659	*Trigonarca* sp.
CNRST-SUNY 81	134660	?*Venericardia* spp.
CNRST-SUNY 82	134661	?*Venericardia* spp.
CNRST-SUNY 84	134662	Ostreida indet.
CNRST-SUNY 85	134663	*Trigonarca* sp.
CNRST-SUNY 86	134658	*Echinotiara perebaskinei*
CNRST-SUNY 89	134664	?*Venericardia* spp.
CNRST-SUNY 90	134665	Ostreidae indet.
CNRST-SUNY 94	22226	*Schizorhiza stroemeri*
CNRST-SUNY 95	22227	*Stephanodus lybicus*
CNRST-SUNY 97a	22228	*Stephanodus lybicus*
CNRST-SUNY 98	134672	*Trigonarca* sp.
CNRST-SUNY 99	134673	Ostreidae indet

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 100	134674	?*Venericardia* spp.
CNRST-SUNY 101	134675	Ostreidae indet.
CNRST-SUNY 103	134676	*Echinotiara perebaskinei*
CNRST-SUNY 104	134677	?*Venericardia* spp.
CNRST-SUNY 105	134678	Ostreida indet.
CNRST-SUNY 106	134679	Lucinidae indet.
CNRST-SUNY 107	134680	Cardiidae indet.
CNRST-SUNY 108	134681	?*Venericardia* spp.
CNRST-SUNY 109	134682	?*Venericardia* spp.
CNRST-SUNY 114	134655	Turritellinae indet. "C"
CNRST-SUNY 122	134656	? Unionidae indet.
CNRST-SUNY 128	134573	Ostreida indet.
CNRST-SUNY 129	134657	*Libycoceras* sp.
CNRST-SUNY 131	22032	*Brychaetus sp.*
CNRST-SUNY 134	134654	*Teredolites clavatus*
CNRST-SUNY 138	22229	*Stephanodus lybicus*
CNRST-SUNY 141	134684	?Stromboidea indet.
CNRST-SUNY 142	134685	?Stromboidea indet.
CNRST-SUNY 144	134579	*Raetomya schweinfurthi*
CNRST-SUNY 145	134581	Ostreida indet.
CNRST-SUNY 146	134582	Ostreida indet.
CNRST-SUNY 148	134574	?*Plicatula* sp.
CNRST-SUNY 149	134686	?Stromboidea
CNRST-SUNY 153	134580	*Crommium nigeriense*
CNRST-SUNY 158	134650	echinoid
CNRST-SUNY 159	134651	*Crommium nigeriense*
CNRST-SUNY 162	134652	*Linthia sudanensis*
CNRST-SUNY 171	134653	*Linthia sudanensis*
CNRST-SUNY 176	134567	*Libycoceras* sp.
CNRST-SUNY 177a	134569	?*Calyptraphorus* sp.
CNRST-SUNY 177d	134570	?*Euspira* sp.
CNRST-SUNY 178a	134571	?*Venericardia* spp.
CNRST-SUNY 178b	134572	?*Venericardia* spp.
CNRST-SUNY 179	134568	*Echinotiara perebaskinei*
CNRST-SUNY 190	33354	*Rhabdognathus keiniensis*

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 191	22252	*Lavocatodus giganteus*
CNRST-SUNY 192	22253	*Lavocatodus giganteus*
CNRST-SUNY 193	22254	*Lavocatodus giganteus*
CNRST-SUNY 199	33308	*Acleistochyles maliensis*
CNRST-SUNY 256	134641	*Gastrochaenolites ornatus* in phosphatic clast
CNRST-SUNY 257	134642	*Gastrochaenolites ornatus* in phosphatic clast
CNRST-SUNY 258	134643	*Gastrochaenolites ornatus* in phosphatic clast
CNRST-SUNY 259	22132	*Brychaetus* sp.
CNRST-SUNY 260	22133	*Brychaetus* sp.
CNRST-SUNY 261	33314	*Palaeophis colossaeus*
CNRST-SUNY 264	22134	*Protopterus elongus*
CNRST-SUNY 265	22135	*Pycnodus zeaformis*
CNRST-SUNY 266	22136	*Pycnodus maliensis*
CNRST-SUNY 267	33315	Dyrosauridae
CNRST-SUNY 268	22137	*Maliamia gigas*
CNRST-SUNY 272c	22138	*Lavocatodus giganteus*
CNRST-SUNY 273b	22139	*Lavocatodus giganteus*
CNRST-SUNY 274c	22140	*Lavocatodus giganteus*
CNRST-SUNY 275	33316	*Phosphatosaurus gavialodes*
CNRST-SUNY 276	33383	*Rhabdognathus keiniensis*
CNRST-SUNY 277	33384	*Rhabdognathus keiniensis*
CNRST-SUNY 278	33311	Hyposaurinae
CNRST-SUNY 279	33309	cf. *Sokotosuchus (new species)* Phosphatosaurinae
CNRST-SUNY 280	33385	*Chenanisuchus lateroculi*
CNRST-SUNY 284	33355	Hyposaurinae
CNRST-SUNY 288	33342	*Palaeophis colossaeus*
CNRST-SUNY 289	33343	*Palaeophis colossaeus*
CNRST-SUNY 290	33344	*Palaeophis colossaeus*
CNRST-SUNY 291	33345	*Palaeophis colossaeus*

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 292	33346	*Palaeophis colossaeus*
CNRST-SUNY 293	33347	*Palaeophis colossaeus*
CNRST-SUNY 294	33348	*Palaeophis colossaeus*
CNRST-SUNY 295	33349	*Palaeophis colossaeus*
CNRST-SUNY 296	33317	*Palaeophis colossaeus*
CNRST-SUNY 297	33318	*Palaeophis colossaeus*
CNRST-SUNY 298	33319	*Palaeophis colossaeus*
CNRST-SUNY 299	33320	*Palaeophis colossaeus*
CNRST-SUNY 300	33321	*Palaeophis colossaeus*
CNRST-SUNY 301	33322	*Palaeophis colossaeus*
CNRST-SUNY 302	33323	*Palaeophis colossaeus*
CNRST-SUNY 303	33324	*Palaeophis colossaeus*
CNRST-SUNY 304	33325	*Palaeophis colossaeus*
CNRST-SUNY 305	33326	*Palaeophis colossaeus*
CNRST-SUNY 306	33327	*Palaeophis colossaeus*
CNRST-SUNY 307	33350	*Palaeophis colossaeus*
CNRST-SUNY 308	33351	*Palaeophis colossaeus*
CNRST-SUNY 309	33352	*Palaeophis colossaeus*
CNRST-SUNY 310	33353	*Palaeophis colossaeus*
CNRST-SUNY 311	33328	*Palaeophis colossaeus*
CNRST-SUNY 312	33329	*Palaeophis colossaeus*
CNRST-SUNY 313	33330	*Palaeophis colossaeus*
CNRST-SUNY 314	33331	*Palaeophis colossaeus*
CNRST-SUNY 315	33332	*Palaeophis colossaeus*
CNRST-SUNY 316	33333	*Palaeophis colossaeus*
CNRST-SUNY 317	33334	*Palaeophis colossaeus*
CNRST-SUNY 318	33335	*Palaeophis colossaeus*
CNRST-SUNY 319	33336	*Palaeophis colossaeus*
CNRST-SUNY 320	33337	*Palaeophis colossaeus*
CNRST-SUNY 321	33338	*Palaeophis colossaeus*
CNRST-SUNY 322	33339	*Palaeophis colossaeus*
CNRST-SUNY 323	33340	*Palaeophis colossaeus*
CNRST-SUNY 324	33313	*Serpenties indet.*
CNRST-SUNY 325	33341	*Palaeophis colossaeus*
CNRST-SUNY 343	22255	*Pycnodus jonesae*
CNRST-SUNY 344	22055	*Pycnodus maliensis*
CNRST-SUNY 345	22056	*Pycnodus zeaformis*
CNRST-SUNY 346	22057	*Pycnodus zeaformis*
CNRST-SUNY 347	22058	*Pycnodus* sp.
CNRST-SUNY 348	22059	*Pycnodus* sp.
CNRST-SUNY 349	22060	*Pycnodus zeaformis*
CNRST-SUNY 350	22054	*Pycnodus zeaformis*
CNRST-SUNY 351	22256	*Pycnodus jonesae*
CNRST-SUNY 352	22047	*Pycnodus jonesae*
CNRST-SUNY 353	22061	*Pycnodus* sp.
CNRST-SUNY 354	22062	*Pycnodus* sp.
CNRST-SUNY 355	22048	*Pycnodus jonesae*
CNRST-SUNY 356	22257	*Pycnodus jonesae*
CNRST-SUNY 357	33356	Hyposaurinae
CNRST-SUNY 358	33357	Hyposaurinae
CNRST-SUNY 360	33358	Hyposaurinae
CNRST-SUNY 361	33359	Hyposaurinae
CNRST-SUNY 363	33360	Hyposaurinae
CNRST-SUNY 364	33361	Hyposaurinae
CNRST-SUNY 365	33362	Hyposaurinae
CNRST-SUNY 366	33363	Hyposaurinae
CNRST-SUNY 374c	22268	*Pycnodus* sp.
CNRST-SUNY 375b	22269	?Sparidae
CNRST-SUNY 377	33364	Hyposaurinae
CNRST-SUNY 381	33365	Hyposaurinae
CNRST-SUNY 383d	22127	Claroteidae (new taxon)
CNRST-SUNY 383e	22128	*Stratodus apicalis*
CNRST-SUNY 384b	22077	Claroteidae (new taxon)
CNRST-SUNY 384c	22078	Claroteidae (new taxon)
CNRST-SUNY 384d	22079	*Pycnodus sp.*
CNRST-SUNY 384e	22080	*Pycnodus jonesae*
CNRST-SUNY 385a	22129	Claroteidae (new taxon)

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 385b	22130	Claroteidae (new taxon)
CNRST-SUNY 385c	22274	Claroteidae (new taxon)
CNRST-SUNY 386	22201	*Protopterus elongus*
CNRST-SUNY 386b	22203	*Protopterus elongus*
CNRST-SUNY 387	22141	*Maliamia gigas*
CNRST-SUNY 387b	22142	*Maliamia gigas*
CNRST-SUNY 387c	22143	*Maliamia gigas*
CNRST-SUNY 387d	22144	*Maliamia gigas*
CNRST-SUNY 388	22202	*Protopterus elongus*
CNRST-SUNY 388b	22204	*Protopterus elongus*
CNRST-SUNY 388c	22205	*Protopterus elongus*
CNRST-SUNY 388d	22206	*Protopterus elongus*
CNRST-SUNY 389	22123	*Protopterus elongus*
CNRST-SUNY 390	22124	*Brychaetus* sp.
CNRST-SUNY 390b	22131	*Brychaetus* sp.
CNRST-SUNY 397b	145893	"Plesielephantiformes"
CNRST-SUNY 400	33310	Hyposaurinae
CNRST-SUNY 412	22045	*Lavocatodus giganteus*
CNRST-SUNY 415	22046	*Eotorpedo hilgendorfi*
CNRST-SUNY 449b	22033	*Pycnodus maliensis*
CNRST-SUNY 449c	22034	*Pycnodus jonesae*
CNRST-SUNY 450d	22225	*Lavocatodus giganteus*
CNRST-SUNY 454	22049	*Lavocatodus giganteus*
CNRST-SUNY 455	22050	*Lavocatodus giganteus*
CNRST-SUNY 457	22051	*Lavocatodus giganteus*
CNRST-SUNY 462	33312	*Amananulum sanogoi*
CNRST-SUNY 471	134583	?*Deltoidonautilus* sp.
CNRST-SUNY 472	134587	?*Cimomia* sp.
CNRST-SUNY 473	134605	Nautiloidea indet.
CNRST-SUNY 474	134666	*Cimomia reymenti*
CNRST-SUNY 475	134629	*Cimomia ogbei*
CNRST-SUNY 476	134644	*Cimomia ogbei*
CNRST-SUNY 480	134599	*Tibia* sp.
CNRST-SUNY 481	134600	*Tibia* sp.
CNRST-SUNY 483	134606	?Stromboidea indet
CNRST-SUNY 484	134584	?*Polinices* sp.
CNRST-SUNY 485	134607	Eocypraeidae indet.
CNRST-SUNY 486	134608	Eocypraeidae indet.
CNRST-SUNY 489a	134630	Turritellinae indet. "A"
CNRST-SUNY 489b	134631	Turritellinae indet. "A"
CNRST-SUNY 489c	134632	Turritellinae indet. "A"
CNRST-SUNY 490	134601	Turritellinae indet. "B"
CNRST-SUNY 492	134609	*Heligmotoma ?oluwolei*
CNRST-SUNY 494a	134625	?*Pseudoliva* sp.
CNRST-SUNY 494b	134626	?*Pseudoliva* sp.
CNRST-SUNY 495a	134627	?*Pseudoliva* sp.
CNRST-SUNY 495b	134628	?*Pseudoliva* sp.
CNRST-SUNY 496	134602	?*Athleta* sp. "B"
CNRST-SUNY 497	134610	?Unionidae indet.
CNRST-SUNY 498a	134633	Ostreida indet.
CNRST-SUNY 498b	134634	Ostreida indet.
CNRST-SUNY 498c	134635	Ostreida indet.
CNRST-SUNY 498d	134636	Ostreida indet.
CNRST-SUNY 501	134645	Ostreida indet.
CNRST-SUNY 506	134603	Trochoidea indet.
CNRST-SUNY 507	134611	?*Athleta* sp. "A"
CNRST-SUNY 508	134612	?*Athleta* sp. "A"
CNRST-SUNY 509	134613	?*Volutilithes* sp.
CNRST-SUNY 510	134614	?*Volutilithes* sp.
CNRST-SUNY 516	134615	Lucinidae indet.
CNRST-SUNY 518	134616	?*Cornulina* sp.
CNRST-SUNY 520	134597	Callocardiinae indet.
CNRST-SUNY 527	134639	?*Venericardia* spp.
CNRST-SUNY 529	134637	?*Venericardia* spp.
CNRST-SUNY 532	134617	?*Athleta* sp. "B"
CNRST-SUNY 533	134618	*Heligmotoma ?oluwolei*
CNRST-SUNY 535	134619	?*Plicatula* sp.
CNRST-SUNY 539	134638	?*Venericardia* spp.
CNRST-SUNY 540	134646	Trochoidea indet.
CNRST-SUNY 541	134620	?Cerithioidea indet.
CNRST-SUNY 542	134621	?Cerithioidea indet.
CNRST-SUNY 543	134585	*Raetomya schweinfurthi*

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 544	134622	*Raetomya schweinfurthi*
CNRST-SUNY 545	134647	*Raetomya schweinfurthi*
CNRST-SUNY 546	134648	*Raetomya schweinfurthi*
CNRST-SUNY 547	134623	?Arcidae indet.
CNRST-SUNY 551	134640	?*Plicatula* sp.
CNRST-SUNY 554	134604	Ostreida indet.
CNRST-SUNY 561	134649	Ostreida indet.
CNRST-SUNY 564A	22122	fish
CNRST-SUNY 565A	22102	fish
CNRST-SUNY 566A	22096	fish
CNRST-SUNY 567A	22081	fish
CNRST-SUNY 568A	22088	fish
CNRST-SUNY 569	22108	fish
CNRST-SUNY 570	134588	*Linthia sudanensis*
CNRST-SUNY 571	134589	*Linthia sudanensis*
CNRST-SUNY 574	134596	*Oriolampas michelini*
CNRST-SUNY 575	134586	*Oriolampas michelini*
CNRST-SUNY 576	595	Fabaceae
CNRST-SUNY 577	596	Fabaceae
CNRST-SUNY 578	597	Fabaceae
CNRST-SUNY 579	134590	*Linthia sudanensis*
CNRST-SUNY 580	134591	*Linthia sudanensis*
CNRST-SUNY 581	134592	*Linthia sudanensis*
CNRST-SUNY 582	134593	*Linthia sudanensis*
CNRST-SUNY 583	134624	*Linthia sudanensis*
CNRST-SUNY 601	134598	*Orlolampas michelini*
CNRST-SUNY 602	134594	*Linthia sudanensis*
CNRST-SUNY 603	134595	*Linthia sudanensis*
CNRST-SUNY 606	145894	"Plesielephantiformes"
CNRST-SUNY 610	22258	fish
CNRST-SUNY 611	22259	fish
CNRST-SUNY 612	22260	fish
CNRST-SUNY 613	22261	fish
CNRST-SUNY 614	22262	fish
CNRST-SUNY 615	22263	fish
CNRST-SUNY 616	22264	fish

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 617	22265	fish
CNRST-SUNY 618	22266	fish
CNRST-SUNY 619	22267	fish
CNRST-SUNY 621	22270	fish
CNRST-SUNY 623	22063	fish
CNRST-SUNY 624	22064	fish
CNRST-SUNY 625	22065	fish
CNRST-SUNY 626	22066	fish
CNRST-SUNY 629	22125	fish
CNRST-SUNY 634	22103	fish
CNRST-SUNY 636	22109	fish
CNRST-SUNY 637	22067	fish
CNRST-SUNY 638	22082	fish
CNRST-SUNY 639	22110	fish
CNRST-SUNY 640	22111	nonteleost fish
CNRST-SUNY 641	22104	nonteleost fish
CNRST-SUNY 642	22097	nonteleost fish
CNRST-SUNY 643	22083	nonteleost fish
CNRST-SUNY 644	22116	nonteleost fish
CNRST-SUNY 645	22089	nonteleost fish
CNRST-SUNY 646	22090	nonteleost fish
CNRST-SUNY 647	22126	fish
CNRST-SUNY 649	22098	nonteleost fish
CNRST-SUNY 650	22091	fish
CNRST-SUNY 650b	22099	fish
CNRST-SUNY 651	22112	nonteleost fish
CNRST-SUNY 652	22105	fish
CNRST-SUNY 653	22068	fish
CNRST-SUNY 654	22113	fish
CNRST-SUNY 664	22118	nonteleost fish
CNRST-SUNY 655	22117	fish
CNRST-SUNY 656	22092	fish
CNRST-SUNY 657	22084	fish
CNRST-SUNY 658	22100	fish
CNRST-SUNY 659	22069	fish
CNRST-SUNY 660	22207	fish
CNRST-SUNY 661	22052	fish
CNRST-SUNY 662	22271	fish

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 663	22085	fish
CNRST-SUNY 665	22106	nonteleost fish
CNRST-SUNY 666	22053	fish
CNRST-SUNY 667	22070	nonteleost fish
CNRST-SUNY 668	22107	nonteleost fish
CNRST-SUNY 669	22119	nonteleost fish
CNRST-SUNY 670	22114	nonteleost fish
CNRST-SUNY 671	22101	nonteleost fish
CNRST-SUNY 672	22093	nonteleost fish
CNRST-SUNY 673	22043	fish
CNRST-SUNY 674	22044	fish
CNRST-SUNY 680	22071	*Brychaetus*
CNRST-SUNY 681	22273	*Brychaetus*
CNRST-SUNY 682	22072	*Brychaetus*
CNRST-SUNY 683	22073	*Brychaetus*
CNRST-SUNY 684	22074	*Brychaetus*
CNRST-SUNY 686	22075	*Stratodus apicalis*
CNRST-SUNY 687	22076	*Stratodus apicalis*
CNRST-SUNY 688	22120	*Stratodus apicalis*
CNRST-SUNY 689	22094	*Stratodus apicalis*
CNRST-SUNY 690	22095	*Brychaetus* sp.
CNRST-SUNY 691	22121	*Cylindracanthus*
CNRST-SUNY 692	22086	*Maliamia gigas*
CNRST-SUNY 792	33366	Hyposaurinae
CNRST-SUNY 793	33367	Hyposaurinae
CNRST-SUNY 794	33368	Hyposaurinae
CNRST-SUNY 795	33369	Hyposaurinae
CNRST-SUNY 796	33370	Hyposaurinae
CNRST-SUNY 797	33371	Hyposaurinae
CNRST-SUNY 798	33372	Hyposaurinae
CNRST-SUNY 799	33373	Hyposaurinae
CNRST-SUNY 800	33374	Hyposaurinae
CNRST-SUNY 801	33375	Hyposaurinae
CNRST-SUNY 802	33376	Hyposaurinae
CNRST-SUNY 803	33377	Hyposaurinae
CNRST-SUNY 804	33378	Hyposaurinae
CNRST-SUNY 805	33379	Hyposaurinae
CNRST-SUNY 806	33380	Hyposaurinae
CNRST-SUNY 807	33381	Hyposaurinae
CNRST-SUNY 808	33382	Hyposaurinae
CNRST-SUNY 809	22115	*Stradodus apicalis*
CNRST-SUNY 810	22087	*Stratodus apicalis*
CNRST-SUNY 812	22039	*Eotrigonodon jonesi*
CNRST-SUNY 813	22040	*Eotrigonodon jonesi*
CNRST-SUNY 814	22218	*Stephanodus lybicus*
CNRST-SUNY 815	22219	*Stephanodus lybicus*
CNRST-SUNY 184	22272[1]	fish
CNRST-SUNY 200	22145[1]	fish
CNRST-SUNY 201	22146[1]	fish
CNRST-SUNY 202	22147[1]	fish
CNRST-SUNY 203	22148[1]	fish
CNRST-SUNY 204	22149[1]	fish
CNRST-SUNY 205	22150[1]	fish
CNRST-SUNY 206	22151[1]	fish
CNRST-SUNY 207	22152[1]	fish
CNRST-SUNY 208	22153[1]	fish
CNRST-SUNY 209	22154[1]	fish
CNRST-SUNY 210	22155[1]	fish
CNRST-SUNY 211	22156[1]	fish
CNRST-SUNY 212	22157[1]	fish
CNRST-SUNY 213	22158[1]	fish
CNRST-SUNY 214	22159[1]	fish
CNRST-SUNY 215	22160[1]	fish

[1] A secondary ichnofossil, *Gastrochaenolites ornatus*, is also present on this specimen.

Original Number	AMNH Specimen number	Taxon
CNRST-SUNY 216	22161[1]	fish
CNRST-SUNY 217	22162[1]	fish
CNRST-SUNY 218	22163[1]	fish
CNRST-SUNY 219	22164[1]	fish
CNRST-SUNY 220	22165[1]	fish
CNRST-SUNY 221	22166[1]	fish
CNRST-SUNY 222	22167[1]	fish
CNRST-SUNY 223	22168[1]	fish
CNRST-SUNY 224	22169[1]	fish
CNRST-SUNY 225	22170[1]	fish
CNRST-SUNY 226	22171[1]	fish
CNRST-SUNY 227	22172[1]	fish
CNRST-SUNY 228	22173[1]	fish
CNRST-SUNY 229	22174[1]	fish
CNRST-SUNY 230	22175[1]	fish
CNRST-SUNY 231	22176[1]	fish
CNRST-SUNY 232	22177[1]	fish
CNRST-SUNY 233	22178[1]	fish
CNRST-SUNY 234	22179[1]	fish
CNRST-SUNY 235	22180[1]	fish
CNRST-SUNY 236	22181[1]	fish
CNRST-SUNY 237	22182[1]	fish
CNRST-SUNY 238	22183[1]	fish
CNRST-SUNY 239	22184[1]	fish
CNRST-SUNY 240	22185[1]	fish
CNRST-SUNY 241	22186[1]	fish
CNRST-SUNY 242	22187[1]	fish
CNRST-SUNY 243	22188[1]	fish
CNRST-SUNY 244	22189[1]	fish
CNRST-SUNY 245	22190[1]	fish
CNRST-SUNY 246	22191[1]	fish
CNRST-SUNY 247	22192[1]	Claroteidae
CNRST-SUNY 248	22193[1]	*Protopterus elongus*
CNRST-SUNY 249	22194[1]	fish
CNRST-SUNY 250	22195[1]	fish
CNRST-SUNY 251	22196[1]	fish
CNRST-SUNY 252	22197[1]	fish
CNRST-SUNY 253	22198[1]	fish
CNRST-SUNY 254	22199[1]	fish
CNRST-SUNY 255	22200[1]	fish
CNRST-SUNY 285	33387[2]	Dyrosauridae
CNRST-SUNY 286	33389[2]	Dyrosauridae
CNRST-SUNY 287	33388[2]	Dyrosauridae
CNRST-SUNY 335	33386[3]	Dyrosauridae

[2] The ichnofossil *Linichnus serratus* is also present on this specimen.

[3] The ichnofossils *Linichnus serratus* and *Knethichnus parallelum* are also present on this specimen.

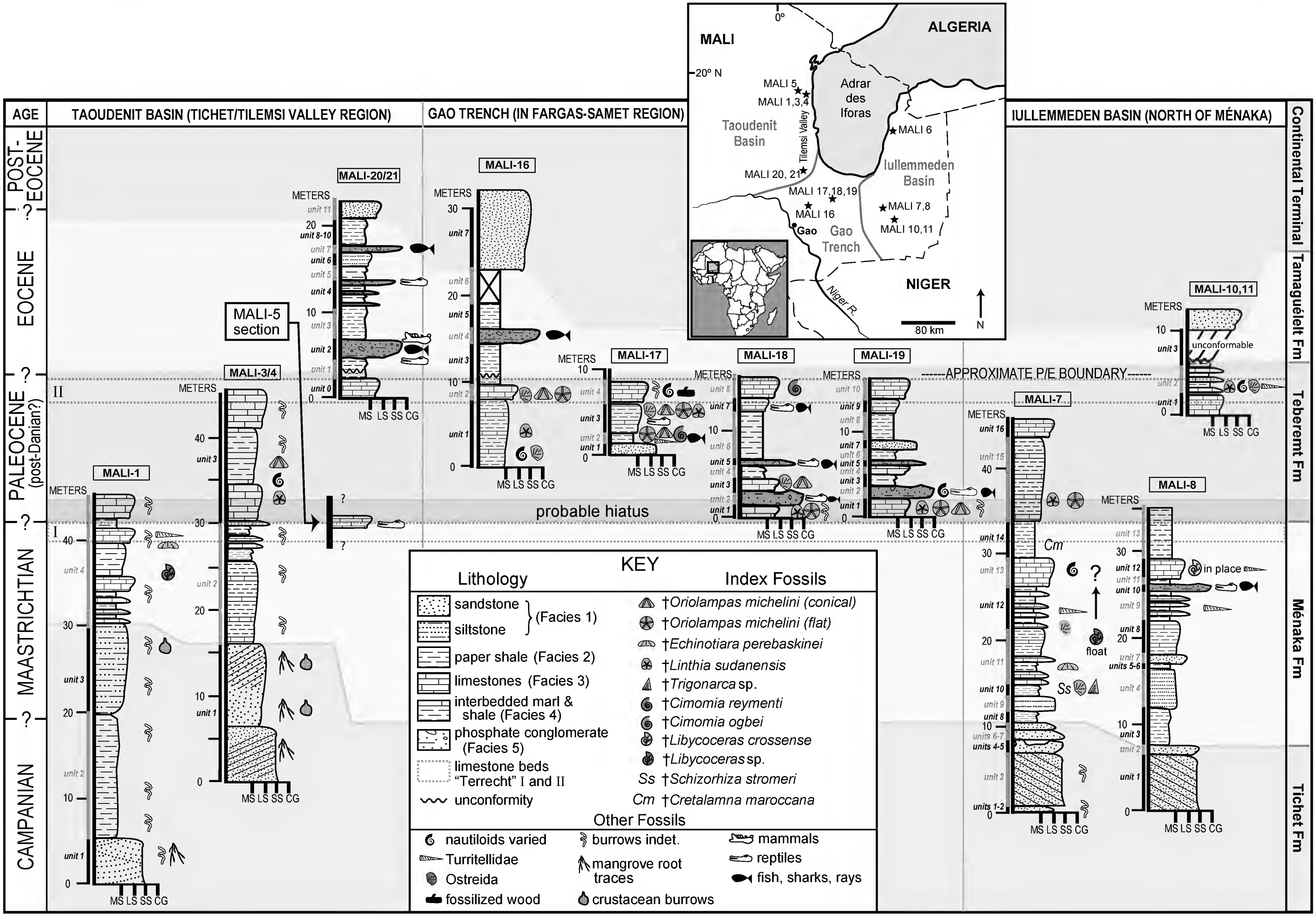


PLATE 1. Correlated stratigraphic section across the Iullemmeden and Taoudenit Basins and the Gao Trench based on our measured sections. "Terrecht I" (I) and "Terrecht II" (II) are distinctive limestone horizons (Radier, 1959). The placement of locality Mali-5 is based on its observed position near "Terrecht 1." Additional fossils such as coprolites and the ichnogenera *Thalassinoides*, *Gastrochaenolites*, *Teredolites*, *Skolithos*, and *Linichnus* are described in the text but not included here due to space constraints. Red lines on map distinguish the three main study regions.

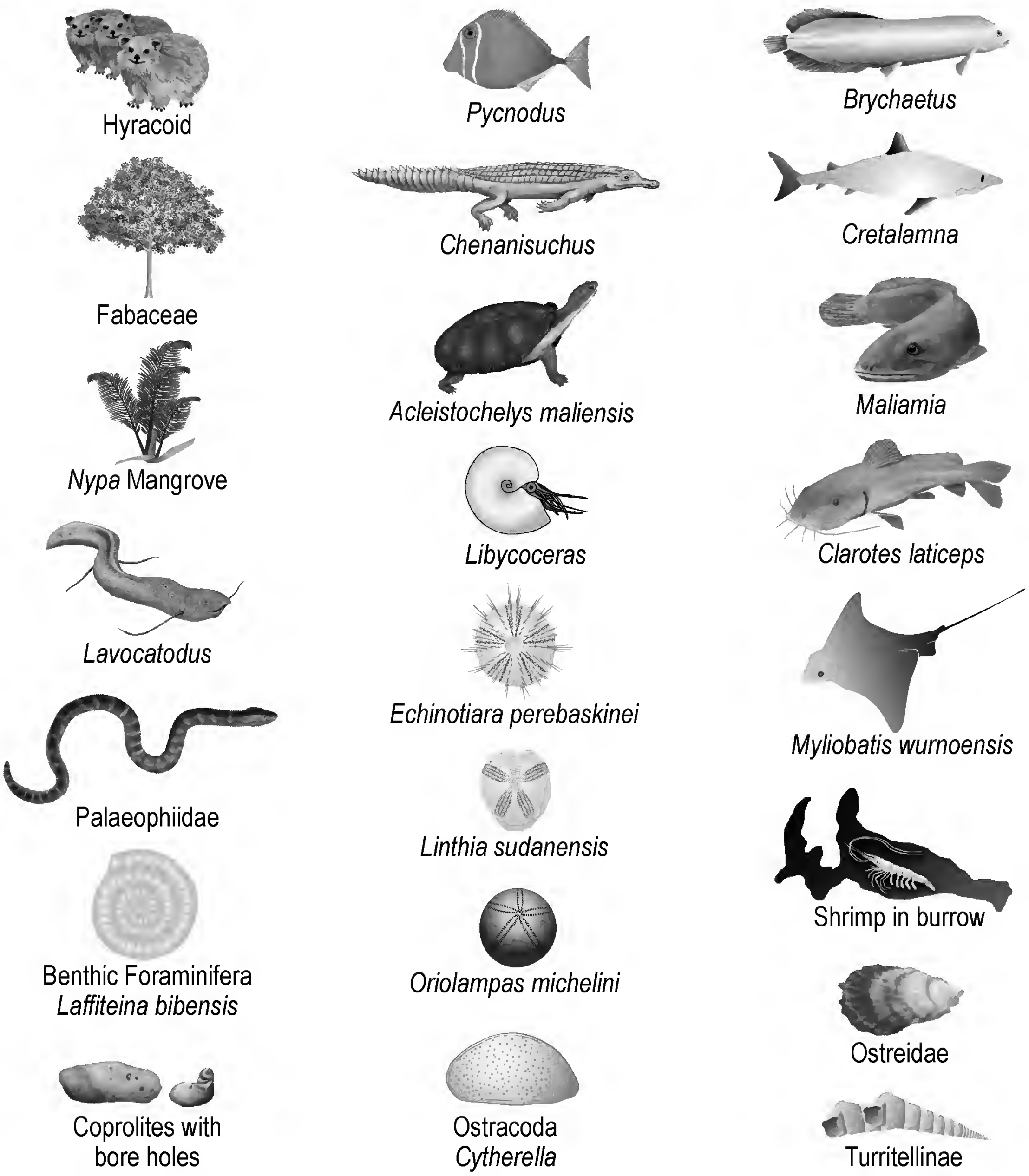
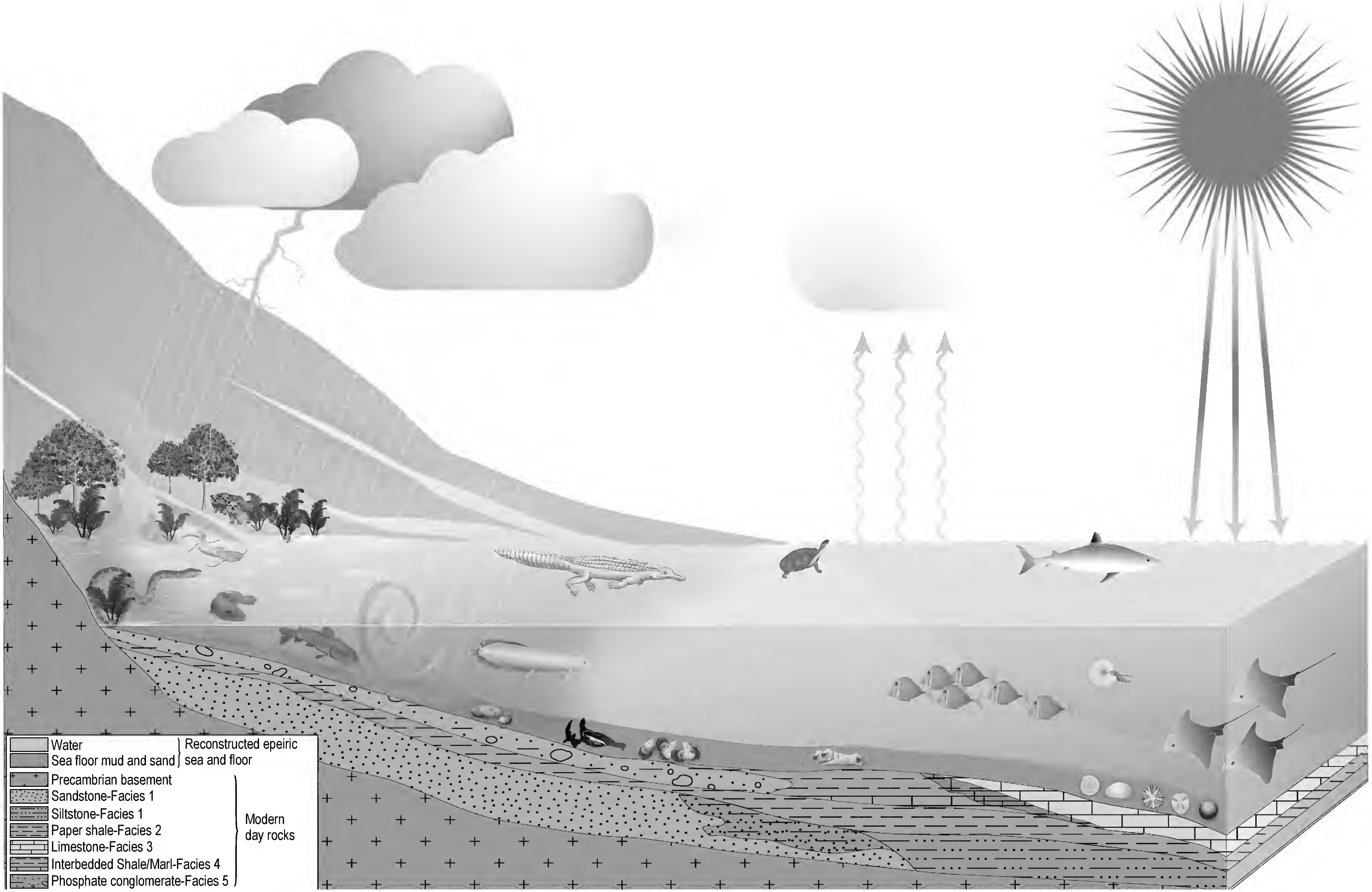


PLATE 2. Schematic environmental reconstruction of the Trans-Saharan Seaway with its fauna and flora overlying the rocks it left behind as described according to our generalized facies model. The seaway was likely limited to the neritic and sunlit benthic zones. Siliciclastic facies (e.g., sandstones) are near shore (proximal) and close to source material eroding from the adjacent Adrar des Iforas massif. Freshwater influence would have been highest here and storm and wave turbulence disturbed the sea floor as indicated by the arrows. Distal facies are mudstones and shales laid down in deeper water. The deepest water had open marine salinity resulting in limestone deposition created by plankton of the photic zone. Water depth did not exceed 50 m. The sandstone (Facies 1) and phosphate conglomerate (Facies 5) deposits were probably not present at the same time. Species are not to scale.


Water
Sea floor mud and sand
Reconstructed epeiric sea and floor
Precambrian basement
Sandstone-Facies 1
Siltstone-Facies 1
Paper shale-Facies 2
Limestone-Facies 3
Interbedded Shale/Marl-Facies 4
Phosphate conglomerate-Facies 5
Modern day rocks

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ON THE COVER: RECONSTRUCTION OF THE TRANS-SAHARAN SEAWAY.